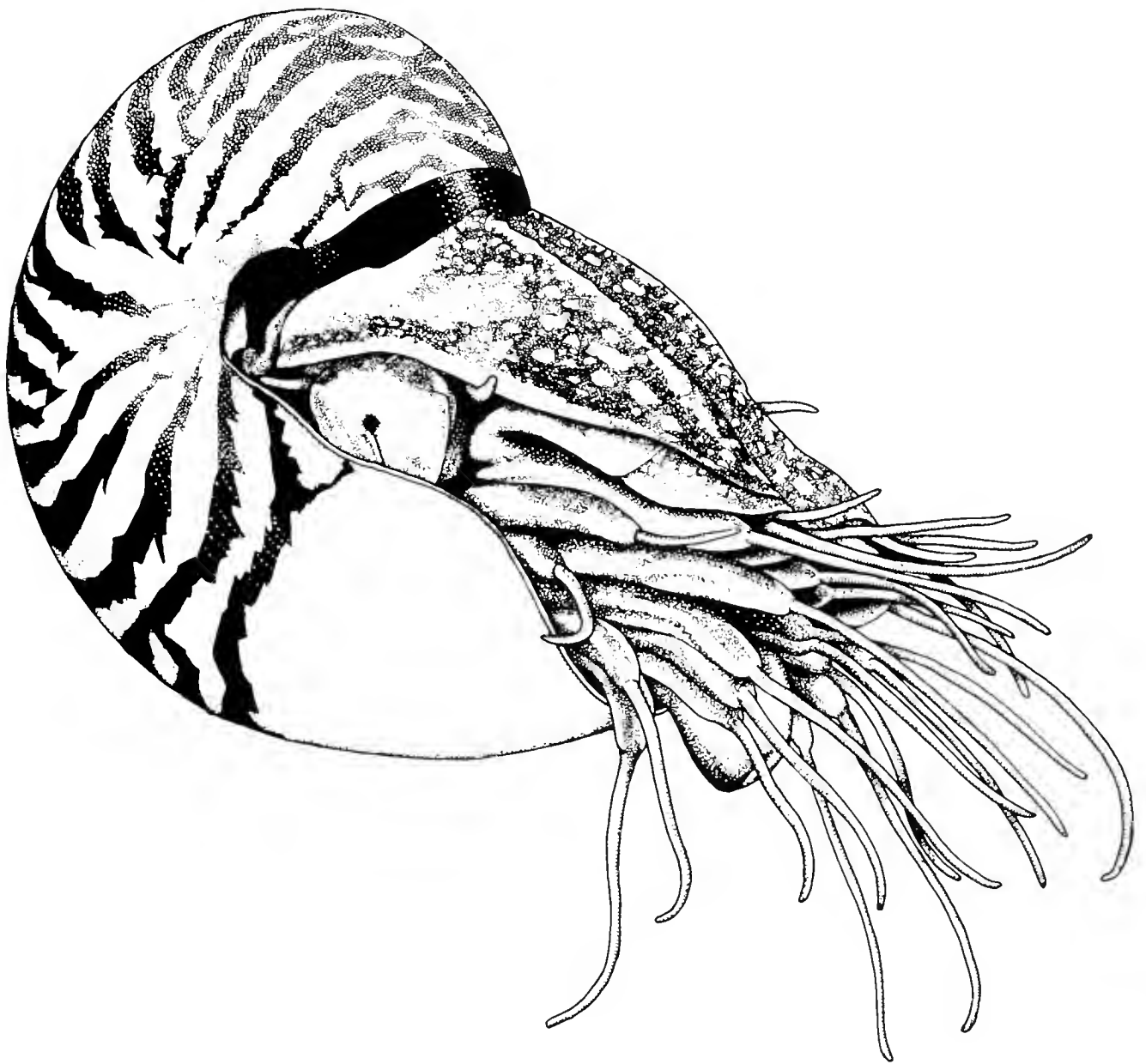


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Spermatogenesis in *Perotrochus quoyanus* (Fischer & Bernardi) (Gastropoda: Pleurotomariidae)

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ABSTRACT

The male reproductive system, ultrastructure of spermatozoa and spermatogenesis are described for the pleurotomariid *Perotrochus quoyanus* (Fischer & Bernardi). Gross morphology of the male reproductive system of *P. quoyanus* agrees in all essential details with that of *Mikadotrochus beyrichii*. In all features, spermatozoa of *Perotrochus quoyanus* closely resemble those of *Perotrochus uestralis* Whitehead, 1987, as well as spermatozoa of certain members of the Trochoidea (Trochidae, Liotidae). Spermatozoa of *P. quoyanus* have a conical acrosomal vesicle with a finely ridged anterior layer, a short, rod-shaped nucleus with numerous lacunae, a midpiece consisting of five (rarely four) mitochondria surrounding a pair of centrioles, a rootlet connecting the centrioles and axoneme to the nucleus, and a flagellum (55–58 μm long) that is continuous with the distal centriole. Investigated species of Haliotidae and Scissurellidae (*Sinezona* sp.) differ from *Perotrochus* in acrosomal substructure, and, in the case of *Sinezona*, also in midpiece and nuclear morphology.

Key Words. Spermatozoa, Spermatogenesis, Mollusca, Gastropoda, Pleurotomariidae, *Perotrochus*, male reproductive tract

INTRODUCTION

Living species of the Pleurotomariidae have a host of primitive gastropod features including a prominent labial shell slit as well as paired gills, auricles, osphradia, kidneys, and hypobranchial glands (Woodward, 1901; Bouvier & Fischer, 1902; Fretter, 1966; Hickman, 1984; Haszprunar, 1988). The Haliotidae and Scissurellidae, which share these features and classically have been assigned to the Pleurotomarioidea, are now considered sufficiently different from the Pleurotomariidae to warrant their placement into separate superfamilies, while the Pleurotomarioidea is considered most closely related to the Trochoidea based on the shared presence of a glandular urinogenital duct in females (for discussion see Haszprunar, 1988, 1989; McLean, 1989). Basic features of pleurotomariid anatomy, including radular morphology, have been known for more than a century (Dall,

1889; Bouvier & Fischer, 1899, 1902; Pelseneer, 1899; Woodward, 1901; Fretter, 1964, 1966), but it is only in recent years that the advent of deep-sea submersible craft has allowed the biology and habitat of living specimens to be studied in detail and *in situ* (Yonge, 1973; Harasewych *et al.*, 1988, 1992).

The field of comparative spermatology has, over the last twenty years, contributed greatly to the resolution of taxonomic and phylogenetic problems in numerous phyla (Baccetti & Afzelius, 1976; Wirth, 1984; Jamieson, 1987), including the Mollusca (Nishiwaki, 1964; Popham, 1979; Giusti, 1971; Kohnert & Storch, 1984a,b; Koike, 1985; Healy, 1983, 1986, 1988a; Hodgson *et al.*, 1988). Among the Gastropoda, studies of archaeogastropod (*s.l.*) spermatozoa and spermiogenesis (Kohnert & Storch, 1983; Azevedo *et al.*, 1985; Koike, 1985; Hodgson & Bernard, 1988; Healy, 1988b, 1989, 1990a,b) are becoming increasingly important since it is from this broad assemblage that origins for the caenogastropod and euthyneuran groups are sought (Cox, 1960; Ponder, 1973; Haszprunar, 1988). The recent discovery of pronounced sperm dimorphism in the trochoidean *Zalipais laseroni* Kershaw, 1955, including a multi-tailed, oligopyrene paraspermatozoon (Healy, 1990b), has drawn attention to the fact that comparatively little is known of the range of sperm morphologies existing in the Vetigastropoda. Healy (1988b) provided the first ultrastructural information on spermatozoa of the Pleurotomariidae [*Perotrochus uestralis* Whitehead, 1987,¹ as *Pleurotomaria africana* (Tomlin, 1948)], but, because of limitations imposed by the state of preservation of the testes, was unable to trace events of spermatogenesis or give substructural detail of certain sperm features. Using glutaraldehyde-fixed testicular material of *Perotrochus quoyanus*, we present the first ultrastructural study of sperm development in a pleurotomariid gastropod.

¹ For a discussion of the nomenclature of this species, see Wagner and Coomans (1990).

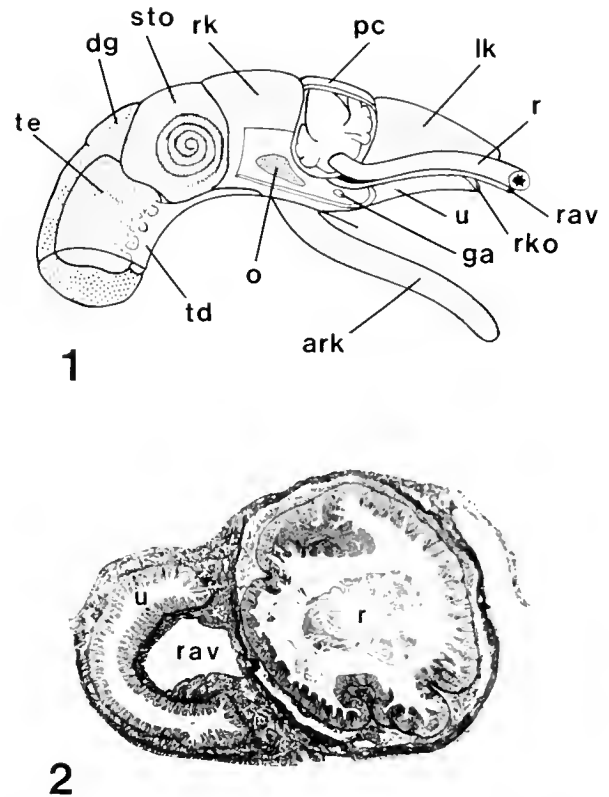
MATERIAL AND METHODS

Three male specimens of the pleurotomariid *Perotrochus quoyanus* (Fischer & Bernardi, 1856) were collected using the research submersible JOHNSON-SEA-LINK II, 103 nautical miles west of Hets-à-Goyaves, off Basse Terre, Guadeloupe, West Indies (16°10'33"N, 61°49'00"W) at a depth of 350–360 m. Specimens were maintained in refrigerated aquaria for six days prior to cracking the shells and excising the testes. For scanning electron microscopy (SEM), samples were prepared by teasing apart sections of fresh testes in filtered seawater, transferring droplets of sperm suspension to coverslips, and fixing with glutaraldehyde vapor (25% glutaraldehyde in a covered petri dish). The coverslips were passed through a graded acetone series (20–100%), critical-point dried, and coated with gold-palladium. The sperm were examined using a Hitachi S-570 SEM at an accelerating voltage of 10 kv. Measurements are based on SEM photographs of sperm and calibration grids of standard size (2160 lines/mm at 15,000 X for acrosomes, nuclei, and mitochondria, 19.7 lines/mm at 1,500 X for tails). For transmission electron microscopy (TEM), 1–2 mm³ pieces of testicular tissue were fixed with 5% glutaraldehyde in 0.2 M cacodylate buffer and shipped to the senior author. Upon arrival, samples were further fixed in cold 3% 0.2 M cacodylate-buffered glutaraldehyde and washed thoroughly in cacodylate buffer before being placed into a 1% solution of osmium tetroxide (prepared in 0.2 M cacodylate buffer) for two hours. Tissues were again rinsed in buffer, then dehydrated using an ascending series of ethanols (20–100%). Spurr's epoxy resin was used to embed the tissues (Spurr, 1969). Ultrathin sections were cut with an LKB IV Ultratome, collected on uncoated 200-mesh copper grids, and stained using either the double lead stain of Daddow (1983) or a single lead procedure (20 minutes uranyl acetate, 10 minutes lead citrate). Sections were examined using a Hitachi 300 transmission electron microscope operated at 75 kV. Remaining soft tissues were fixed in 10% formaldehyde in seawater and transferred to 70% ethanol for dissection. Shell fragments retained as voucher specimens are housed in the National Museum of Natural History, Smithsonian Institution (USNM 878154).

RESULTS

MALE REPRODUCTIVE SYSTEM

The mustard-colored testis (fig. 1, te) lines the right wall of the digestive gland (fig. 1, dg), and empties into a thin-walled testicular duct (fig. 1, td) situated ventral to both these organs. This duct becomes tubular along the ventral surface of the stomach (fig. 1, sto) and continues anteriorly, emptying (fig. 1, ga) into the ureter portion of the right kidney (fig. 1, rk) anterior and to the right of the opening (fig. 1, o) of the anterior lobe of the right kidney (fig. 1, ark), which is situated in the cephalic hemocoel. The ureter/urinogenital duct (figs. 1, 2, u) runs anteriorly along the roof of the mantle cavity to the



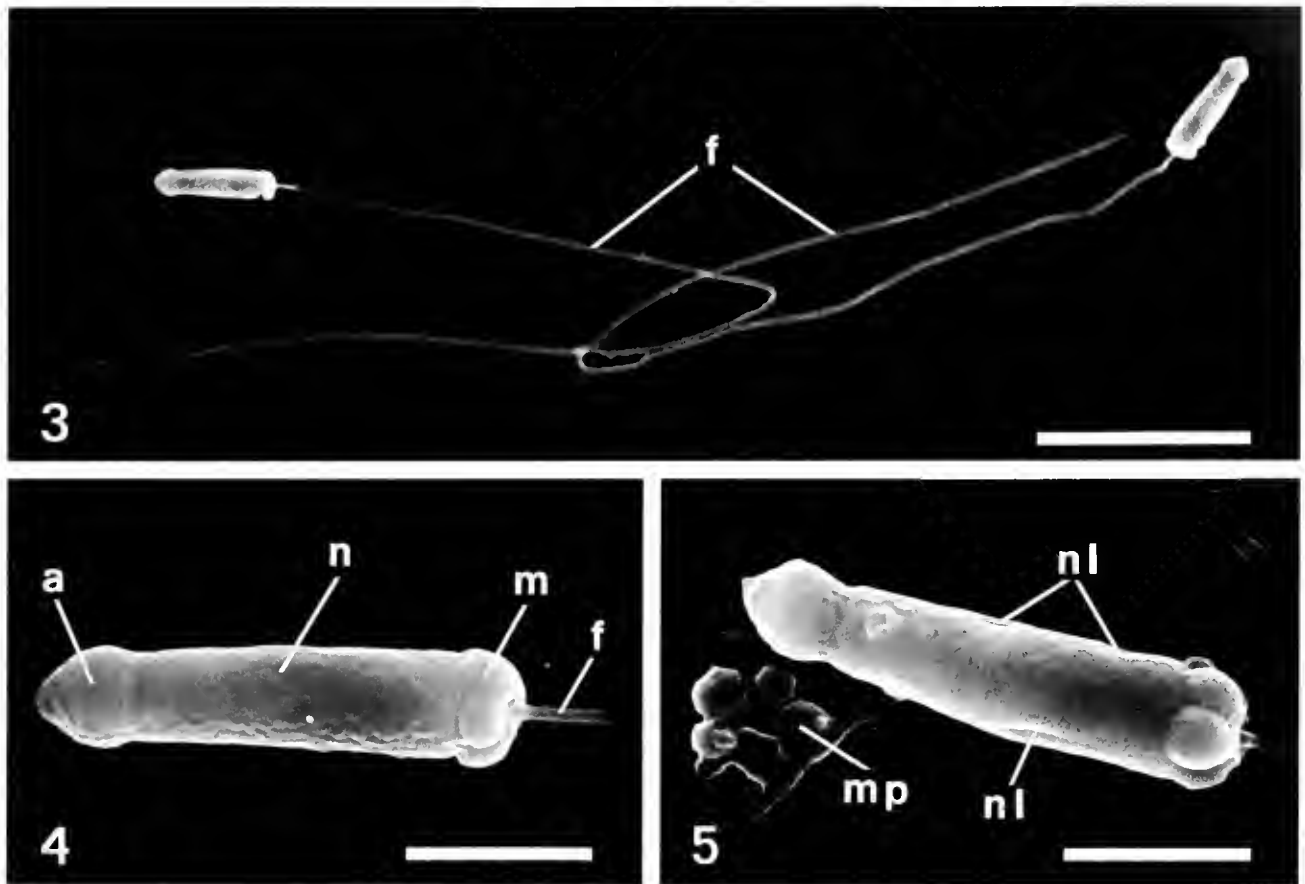
Figures 1–2. Male reproductive tract of *Perotrochus quoyanus* (Fischer & Bernardi). **1.** Diagrammatic representation of male reproductive system, viewed from right side. Walls of pericardium and right kidney removed to reveal contents. **2.** Transverse section midway along pallial gonoduct, viewed from anterior. ark, anterior lobe of right kidney; dg, digestive gland; ga, genital aperture; lk, left kidney; o, opening of anterior lobe of right kidney; pc, pericardium; r, rectum; rav, right afferent branchial vessel; rk, right kidney; rko, right kidney opening; sto, stomach; td, testicular duct; te, testis; u, urinogenital duct.

right of the rectum (figs. 1, 2, r), envelops the right afferent branchial vessel (figs. 1, 2, rav), and drains into the mantle cavity through a transversely oriented right kidney opening (fig. 1, rko), approximately 1/4 of the distance from the rear of the mantle cavity to the rear of the mantle slit. The urinogenital ducts of all three individuals lacked a glandular lining.

The testes of two animals were full of mature spermatozoa, while that of the third animal were almost entirely spent. Although only scattered groups of developing cells remained, we were able to identify basic features of spermatogonia, spermatocytes and spermatozoa.

MATURE TESTICULAR SPERMATOZOA (SEM OBSERVATIONS)

Spermatozoa of *Perotrochus quoyanus* consist of a conical acrosomal complex (fig. 4, a), a rod-shaped nucleus (fig. 4, n), a cluster of five, equal-sized, spherical mitochondria (fig. 4, m, fig. 5, mp) at the base of the nucleus, and a single 55–58 μ m long flagellum (figs. 3–4, f, table



Figures 3–5. *Perotrochus quoyanus*. Mature testicular sperm, SEM. **3.** Two spermatozoa including entire flagella (f). **4,5.** Acrosome (a), nucleus (n) and mitochondria (m) of two spermatozoa. Nuclear lacuna (nl) and detached midpiece (mp) consisting of five mitochondria visible in figure 5. Scale bars: **3** = 10 μm ; **4,5** = 2 μm .

1). The acrosomal complex (externally, the acrosomal vesicle proper) is approximately 1.15 μm long, tapers slightly at contact with the nucleus, and has a maximum diameter of 1.18 μm (figs. 4,5, table 1). The nucleus measures 3.7 μm in length, is broadest posteriorly, with a maximum diameter of 1.4 μm . Irregular indentations on the nuclear surface (fig. 5, nl) can be correlated by TEM with nuclear lacunae (figs. 6, 7, 11, nl) occurring beneath the nuclear and plasma membranes. These indentations are not, therefore, nuclear pores. Spherical mitochondria (diameter 0.8 μm) obscure the attachment site of the flagellum. The flagellum narrows markedly towards its insertion point within the midpiece (figs. 13,15).

MATURE TESTICULAR SPERMATOZOA (TEM OBSERVATIONS)

Acrosome: The acrosomal vesicle is broadly conical, with a rounded anterior surface and flattened basal surface (fig. 7, av). The vesicle has a length of 0.90–0.93 μm and the maximum diameter of 1.28 μm at its base is wider than the apex of the nucleus (figs. 7,8, n). A

deep, narrow invagination extends anteriorly from the base of the vesicle and is filled with a diffuse, faintly fibrous material (figs. 8, 10, sm). Some sections clearly indicate an eccentric, slightly angular alignment for the invagination relative to the sperm longitudinal axis (figs. 8, 10). Beneath the anterior face of the acrosomal vesicle is an electron-lucent layer containing fine ridges with a periodicity of 12–14 nm (figs. 7,9, rl). A similarly electron-lucent layer, lacking discernible ridged substructure, forms the basal rim of the acrosomal vesicle (fig. 7, br). A loose, fibrous deposit of subacrosomal material occupies the space between the base of the acrosomal vesicle and the nuclear apex (fig. 8, sm).

Nucleus: The mature nucleus (fig. 6, n) is short (3.7 μm) and almost cylindrical, with a shallow depression anteriorly (figs. 7, 8, n) and five (rarely four) shallow depressions surrounding a centriolar fossa posteriorly (figs. 14, 15, n). The anterior depression is associated with subacrosomal material (fig. 8, sm), while the posterior depressions act as sockets for the midpiece mitochondria (fig. 15, m). Dense material linking the proximal and

Table 1. Dimensions of mature spermatozoa from SEM observations. Linear measurements in μm ($n = 30$, 10 sperm from each of three individuals)

	Mean	Range	Standard deviation (σ)
Acrosome			
Length	1.10	1.01–1.19	0.07
Width	1.08	1.01–1.18	0.05
Nucleus			
Length	3.67	3.52–3.78	0.08
Width (anterior)	0.98	0.95–1.03	0.02
Width (posterior)	1.19	1.13–1.34	0.05
Mitochondria			
Diameter	0.80	0.68–0.93	0.09
Flagellum			
Length	56.5	52.7–61.1	3.26

distal centrioles is continuous with a hollow rootlet (figs. 14, 15, r), the bulbous end of which fills the centriolar fossa. Numerous irregularly shaped lacunae (figs. 6, 7, 11, nl) occur within the nucleus, some of which open underneath the nuclear membranes, though not to the plasma membrane or cell surface. Nuclear contents are highly electron dense and consist of tightly packed fibers (diameter 16 nm) set in a finely granular matrix.

Midpiece: Five (rarely four) spherical (diameter 0.6–0.8 μm) mitochondria (figs. 12, 15, m), each having curved, plate-like cristae, surround the proximal and distal centrioles to form the sperm midpiece (fig. 12). The centrioles (figs. 14, 15, pc, dc), arranged at a 90° angle to each other, are hollow, cylindrical structures composed of triplet microtubules and embedded in a pericentriolar matrix (triplets often obscured by matrix, see fig. 15 inset). Nine satellite fibers (figs. 15, 16, sf) connect the distal centriole to an annulus (figs. 15, 16, an), a ring-shaped deposit of material lining the inner surface of the plasma membrane. The flagellar axoneme, therefore, is anchored to the midpiece and nucleus via the centrioles and rootlet as well as by the radial set of satellite fibers.

Flagellum: The flagellum measures approximately 55–58 μm in length and consists of a 9+2 axoneme enclosed by the plasma membrane (figs. 15, f; 17). Many spermatozoa were observed with an angularly offset flagellar-centriolar apparatus (fig. 13). This misalignment could be due to tight packing of sperm within the testis or even slight immaturity, since our SEM observations on free

sperm show a normal, posteriorly projecting flagellum (figs. 3–5). Occasionally, a dense body is enclosed with the axoneme by the plasma membrane (fig. 17, db). Its position along the flagellum could not be determined. Further study is required to determine whether this structure is a true sperm feature of *P. quoyanus* or an artifact of fixation. In the distal region of the flagellum, the 9+2 substructure of the axoneme degenerates into singlet microtubules (fig. 17, arrow).

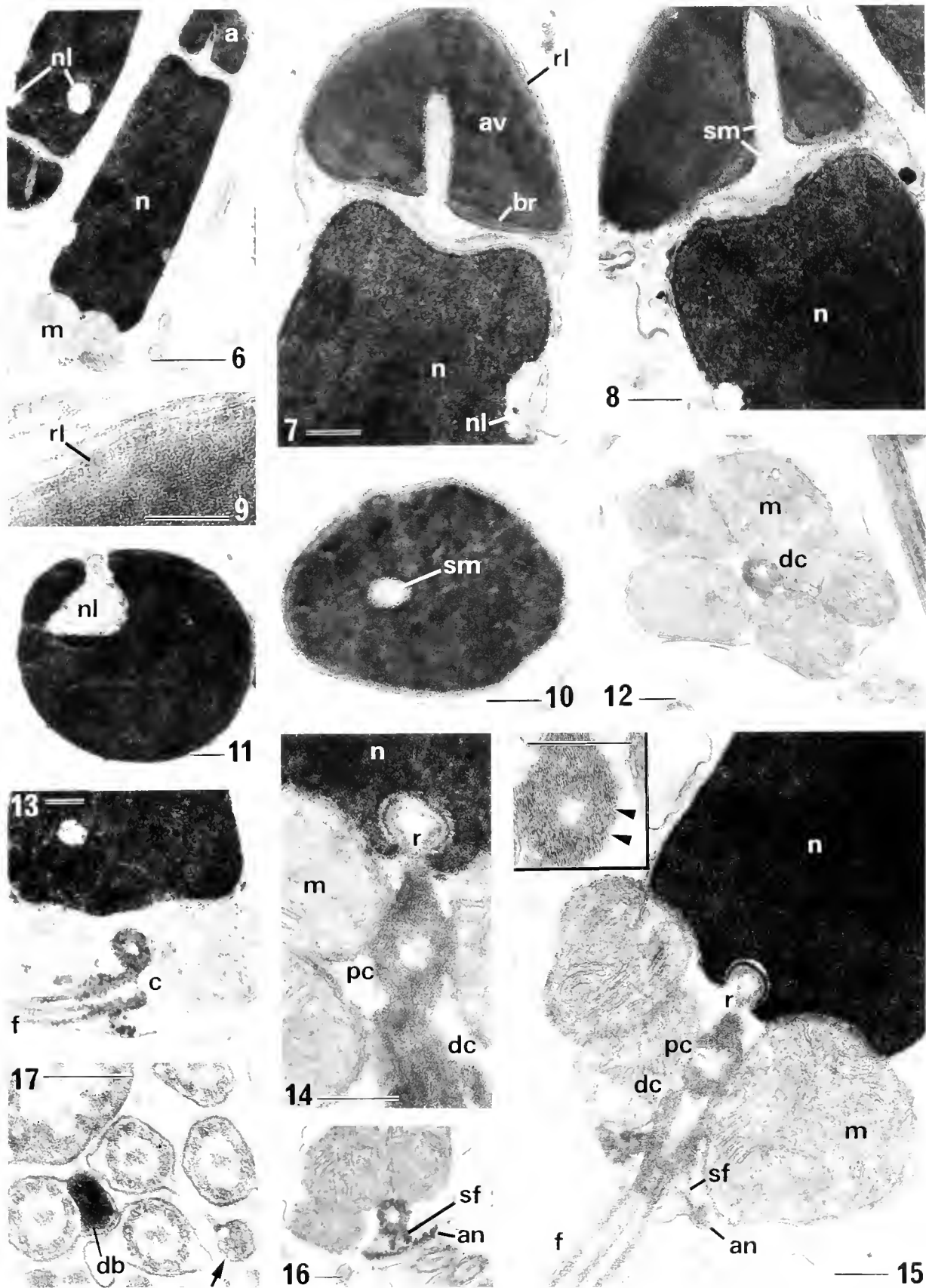
SPERMATOGENESIS

Spermatogenic cells present within the testis consisted principally of isolated clumps of spermatocytes and spermatids (fig. 18, spc, spt). Most of the testis space in ripe males was found to be almost totally occupied by tightly packed mature spermatozoa. To some extent the process of reconstructing events of spermatogenesis was hampered by the occurrence of many abnormally developing spermatocytes and spermatids. The morphology and possible significance of these cells is treated in the final section of these results.

Spermatogonia: Spermatogonia (fig. 19) were only rarely observed. They can be distinguished from spermatocytes and spermatids by their oblong, usually lobulate nucleus (fig. 19, n; length 6.0 μm , breadth 4.0 μm), prominent nucleolus (fig. 19, nc; diameter 0.7 μm), well-developed nuclear pores (fig. 19, arrows), numerous small mitochondria (fig. 19, m; diameter 0.3–0.4 μm), and more extensive cytoplasm. Endoplasmic reticular cisternae, where visible, are scattered and poorly developed. The presence of centrioles and Golgi complex could not be confirmed in the limited number of observed cells.

Spermatocytes: Spermatocytes (fig. 20) have a spherical to ovoid nucleus (fig. 20, n; diameter 4.0–4.5 μm) that appears to lack either a nucleolus or prominent nuclear pores. The small electron-dense patches visible in many cells (fig. 20, arrowheads) may be sites of synaptonemal complexes, although these structures are more easily discerned in moribund spermatocytes that have partially lost nuclear contents (fig. 3S, arrows). Mitochondria (fig. 20, m; diameter 0.6–0.75 μm) markedly larger than those of spermatogonia are pressed slightly into the surface of the nucleus. Highly electron-dense proacrosomal vesicles (fig. 20, pav; diameter 0.1–0.2 μm) of Golgian origin are found throughout the cytoplasm. The axoneme (fig. 21, ax) develops intracellularly from one of a pair of orthogonally arranged centrioles (fig. 21, pc, dc) positioned close to the concave face of the Golgi complex (fig. 21, G). Even at this early stage in axoneme formation, satellite fibers (fig. 21, sf) are associated with the future

Figures 6–17. *Perotrochus quoyanus*. Mature testicular sperm, TEM. **6.** Acrosome (a), nucleus (n), nuclear lacunae (nl), and mitochondria (m) of two spermatozoa. **7, 8.** Acrosomal vesicle (av) showing ridged layer (rl), basal rim (br), subacrosomal material (sm), and apex of nucleus (n) with nuclear lacuna (nl). **9.** Detail of ridged layer (rl) in acrosome. **10.** Transverse section through acrosomal vesicle showing subacrosomal material (sm). **11.** Transverse section through nucleus showing nuclear lacuna (nl). **12.** Transverse section through midpiece, five mitochondria (m) surround the distal centriole (dc). **13.** Angularly offset centriolar (c)—flagellum (f) apparatus of a spermatozoon. **14.** Detail of centriolar fossa and attached rootlet (r), proximal (pc) and distal centrioles



(dc), and mitochondria (m). 15. Base of nucleus (n), rootlet (r), proximal (pc) and distal (dc) centrioles, satellite fibers (sf), annulus (an), flagellum (f), and mitochondria (m). Inset: triplet microtubules of proximal centriole (arrowheads). 16. Oblique section showing distal centriole and three of nine satellite fibers (sf) attached to annulus (an). 17. Transverse section through flagella. Note distal region (right) and dense body (db) (left). Arrow indicates singlet microtubules in distal region of flagellum. Scale bars: 6 = 1 μ m; 7,8,10-17 = 0.25 μ m; 9 = 0.1 μ m.

distal centriole. Endoplasmic reticular cisternae are poorly developed

Spermatids (Spermiogenesis): Spermatids can be divided into three categories based on the condensed state of the nucleus: early cells, middle-stage cells, and advanced spermatids.

In early spermatids the nucleus (fig. 22, n) is spherical with pale-staining, fibrous contents. Middle-stage spermatids (figs. 23, 24) are distinguished from earlier cells by a marked increase in the electron density of the nuclear fibers, and by a tendency of the mitochondria and centrioles to move toward the incipient posterior pole of the nucleus. Although multiple proacrosomal vesicles are still apparent within the cytoplasm of middle-stage spermatids (figs. 24, 25, pav), it is during this phase of spermiogenesis that the definitive acrosomal vesicle is formed by fusion of proacrosomal vesicles. In advanced spermatids, mitochondria and the acrosomal vesicle come to lie in shallow depressions of the nucleus, while the nucleus itself becomes oblong and its constituent fibers more condensed (figs. 26, 27, 36, 37). In addition, the acrosomal vesicle undergoes pronounced changes in shape and substructure. Initially, the acrosomal vesicle is round and underlain by a thin disjointed layer of subacrosomal material (fig. 26, sm). As seen in figure 26, the site of first contact between the definitive acrosomal vesicle and nucleus may occur close to where the mitochondria are situated. Following attachment of the acrosomal vesicle to the condensing nucleus, vesicle contents become differentiated into a cluster of coarse granules (fig. 27, g) and a more extensive homogeneous portion (fig. 27, h). These granules become partitioned into two deposits that occupy anterior and posterior depressions in the homogeneous portion (fig. 28). Subsequently, an invagination of the homogeneous portion, but not the acrosomal membrane, begins to form anteriorly (fig. 29, arrowhead). The anterior cluster of granules transforms into a finely ridged layer (figs. 28–34, rl). As this layer grows, it extends into a deepening invagination of the homogeneous portion (figs. 29–31, arrowhead). The posterior cluster of granules forms the electron-lucent basal rim of the acrosomal vesicle. A thin deposit of dense material defines the basal region of the acrosomal membrane (figs. 28, 29, dm). Late in spermiogenesis, the basal invagination of the acrosomal vesicle develops and is filled with subacrosomal material (fig. 31, sm). The anterior invagination of the homogeneous portion, which is not an invagination of the vesicle membrane, and the basal invagination of the vesicle are distinct and unconnected structures. The anterior invagination ultimately disappears, perhaps by a process of eversion, leaving the ridged electron-lucent layer (figs. 31, 34, 35, rl) and a small electron-lucent plate (figs. 31, 34, 35, asterisk).

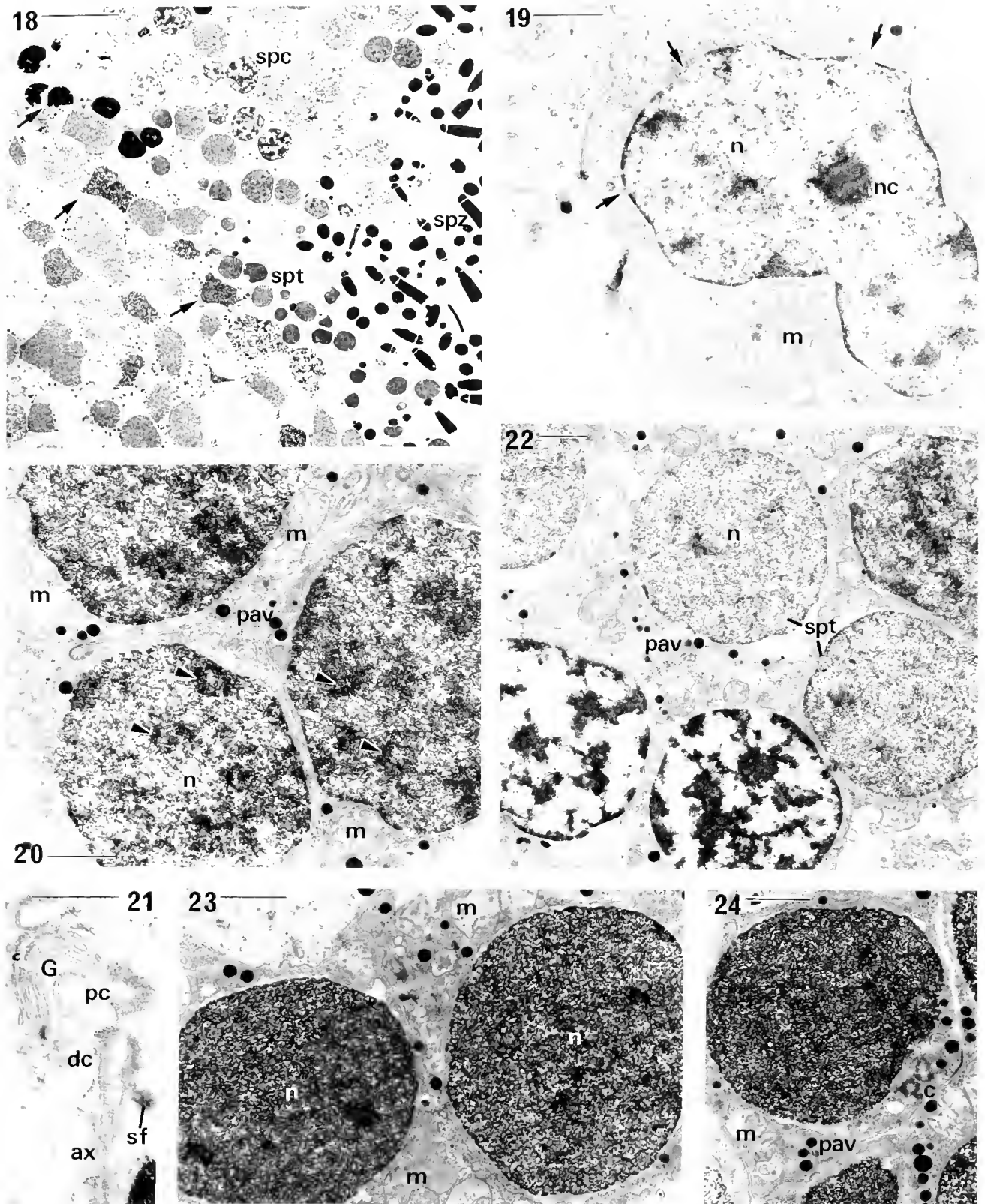
Nuclear lacunae, so clearly apparent in mature testicular spermatozoa, only become evident in the very last stage of spermiogenesis. These spaces are not in contact with the exterior of the spermatid. The centriolar fossa (fig. 36, arrowhead) forms through invagination of the nuclear extension that lies between the posteriorly po-

sitioned mitochondria. Origins of the pericentriolar matrix and centriolar rootlet were not determined. Presumably the centrioles play some role in the growth of these structures.

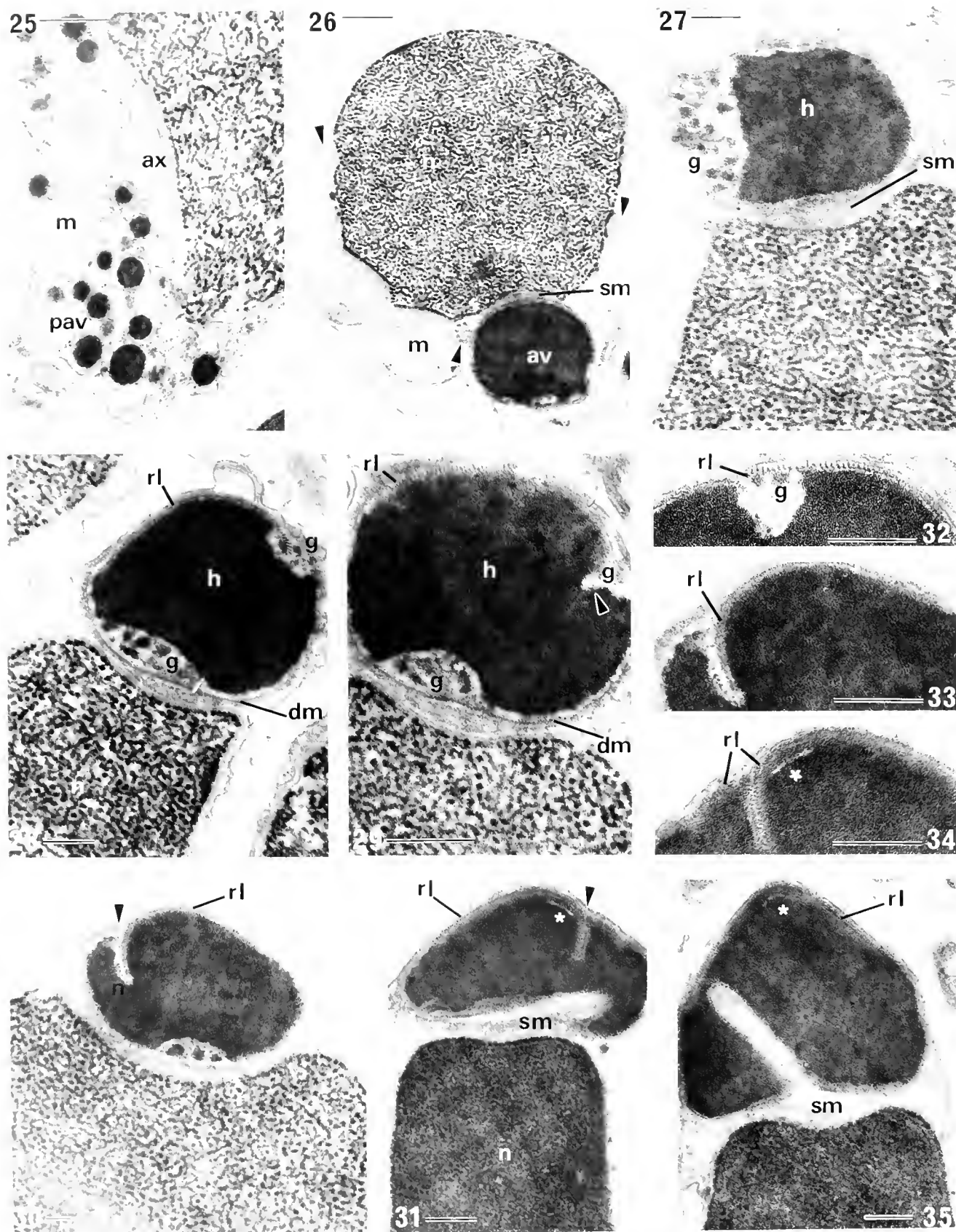
Aberrant spermiogenic cells: In addition to spermatogonia, spermatocytes and spermatids, the testes also contained numerous abnormally developing spermatocytes and spermatids. Some of these spermatocytes appear moribund (fig. 38). The spermatids, however, are clearly recognizable by their angular shape, evidently the result of cytoplasmic pressure from adjacent cells (figs. 18, spt; 39). Nuclear condensation and proacrosomal vesicle production seem to proceed as in normally developing cells. Gradually, however, the nucleus becomes oblong then angular and ultimately irregular in shape (figs. 39–42). Like normal spermatozoa, mature nuclei of the abnormal, presumably abortive, lines have numerous lacunae (fig. 42, nl) and a fibro-granulate substructure (figs. 40–42). The proacrosomal vesicles, rather than forming a definitive acrosomal vesicle, remain as a clump of unfused entities (Figure 40, inset, pav). Mitochondria, located in depressions of the nucleus, and axonemal profiles are often observed in developing and 'mature' aberrant spermatozoa (figs. 40, m; 41, ax). The position and number of centrioles was not determined.

DISCUSSION

Reproductive System: The morphology of the male reproductive system of *Perotrochus quoyanus* agrees in all major features with that of *Mikadotrochus beyrichii*, the only other species of pleurotomariid for which the male reproductive system has been documented (Woodward, 1901). The female reproductive system of pleurotomariids differs from the male reproductive system in that the pallial portion of the right kidney, the urinogenital duct, is glandular. To date, only *M. beyrichii* (Woodward, 1901) and *Perotrochus nidas* (Fretter, 1966) are confirmed to have glandular female urinogenital ducts. The duct of the holotype of *Perotrochus amabilis* (Bayer, 1963), an "immature" female on the basis of gonadal sections, lacked glandular elements, prompting Fretter (1964:179) to suggest that this was a young individual that had never spawned, and that glands may develop in the walls of this duct only as the gonad becomes mature. Examination of the shells of more than a dozen specimens collected in the intervening decades reveals that the holotype of *M. amabilis* is among the larger specimens known of this species. It is therefore unlikely that the holotype is an immature individual. Gonadal development of several western Atlantic pleurotomariids varies with season (Harasewych, unpublished observations), suggesting that the glandular lining of the urinogenital duct of females may develop and diminish cyclically. As evidenced by the three specimens used in this study, the urinogenital ducts of male pleurotomariids are not glandular, even during the spawning season. Nevertheless, absence of a glandular urinogenital duct may



Figures 18–24. *Perotrochus quoyanus* Spermatogenesis. **18.** Survey section of testis showing spermatozoa (spz), developing spermatocytes (spe), and advanced spermatids (spt). Arrows indicate aberrant spermatids. **19.** Spermatogonium. Note lobulate nucleus (n), large nucleolus (nc), nuclear pores (arrows), and numerous small mitochondria (m). **20.** Spermatocytes. Note mitochondria (m), nucleus (n), presence of proacrosomal vesicles (pav), and putative synaptonemal complexes (arrowheads). **21.** Spermatocyte Golgi complex (G) close to proximal and distal centrioles (pc, dc) and axoneme (ax). Note satellite fibres (sf) associated with distal centriole. **22.** Early spermatids (spt) with homogeneously granular nuclei (n) and proacrosomal vesicles (pav). **23.** Middle stage spermatids with very electron dense fibrillar nuclei (n) and mitochondria (m). **24.** Middle stage spermatid showing pair of centrioles (c), proacrosomal vesicles (pav), and mitochondria (m). Scale bars: 18 = 10 μm ; 19, 20, 22–24 = 1 μm ; 21 = 0.5 μm .



Figures 25-35. *Leptotrochus quoyanus*. Acrosome development. 25. Group of proacrosomal vesicles (pav) near mitochondrion (m) and axonemes (ax). 26. Spermatid with acrosomal vesicle (av) contacting nucleus (n) near mitochondrion (m). Subacrosomal

not be a sufficient criterion for identifying male specimens.

Spermatogenesis: Despite the complicating factor of moribund and abnormally developing cells within the testis, spermatogenic stages of *Perotrochus quoyanus* resemble those reported for the Trochoidea (Kohnert & Storch, 1983; Azevedo *et al.*, 1985; Koike, 1985; Healy, 1989). Using museum-preserved tissues, Healy (1988b) was able to determine that acrosomal development in *Perotrochus westralis* involved the production of multiple proacrosomal vesicles. Fusion of proacrosomal vesicles into a definitive acrosomal vesicle has been demonstrated in many bivalves (Longo & Dornfeld, 1967; Kubo, 1977; Bernard & Hodgson, 1985; Hodgson & Bernard, 1986; Eckelbarger *et al.*, 1990), and, outside the Mollusca, in groups as disparate as the Polychaeta (Franzén, 1987) and Echinodermata (Dan & Sirakami, 1971; Chia & Bickell, 1983). In contrast, acrosome development in patelloidean gastropods centers on the production of a single, electron-lucent vesicle to which small vesicles from the Golgi cisternal edges fuse and contribute (Hodgson & Bernard, 1988). Our study has discovered details of acrosome development previously undescribed in the Vetigastropoda, including the differentiation of anterior and posterior extremities of the vesicle and formation of fine ridges in the anterior electron-lucent layer. There are reasons for believing that these events also occur in the Trochoidea. Mature acrosomes of trochids frequently show anterior and posterior electron-lucent layers (the anterior layer with ridges; Healy & Daddow unpublished). In spermatids of *Omphalius pfeifferi* (Philippi, 1846), the definitive acrosomal vesicle (Koike, 1985:plate 3D) closely corresponds to the stage illustrated herein for *Perotrochus quoyanus* (fig. 30). The origin of the subacrosomal material in *P. quoyanus* and in *Gibbula umbilicalis* (da Costa, 1778) (see Azevedo *et al.*, 1985) is unknown. A Golgian source seems unlikely, as this secretory organelle has migrated posteriorly by the time the definitive acrosomal vesicle has formed (the stage when subacrosomal material becomes visible). Possibly, the acrosomal vesicle itself is capable of organizing the accretion or polymerization of extravesicular materials within the cytoplasm. Takaichi & Dan (1977) proposed a similar origin for subacrosomal material in the pulmonate *Euhadra hickonis* (Kobelt, 1879). An interesting feature of spermiogenesis in *Perotrochus quoyanus* is the often distant positioning of the nuclear-contacted acrosomal vesicle

relative to this vesicle's final position at the nuclear apex (see fig. 26). A comparable situation occurs in the trochid *Calliotropis glyptus* (Watson, 1879) (see Healy, 1989) and evidently in the turbinid *Lunella granulata* (Gmelin, 1791) (see micrographs of Koike, 1985). In *Perotrochus*, *Calliotropis*, and *Lunella*, however, the mature acrosomal vesicle lies at the nuclear apex, indicating that by some means, perhaps via nuclear shape change late in spermiogenesis or acrosomal movement, the vesicle attains its final position.

The pattern of nuclear condensation in *Perotrochus quoyanus* differs from that occurring in the Trochoidea in two respects: (1) the heterochromatin forms a homogeneous network of dense fibers, whereas the heterochromatin forms distinct granules in Trochoidea; and (2) nuclear lacunae appear only at the last stage of spermatid development, whereas the lacunae are well developed and visible at earlier stages in Trochoidea (Kohnert & Storch, 1983; Azevedo *et al.*, 1985; Koike, 1985; Healy, unpublished data). Unfortunately, no comparative information exists on nuclear condensation or, in fact, on any aspect of spermiogenesis, in the Haliotidoidea, Scissurelloidea, or Fissurelloidea. Initially the centriolar fossa of *Calliotropis glyptus* spermatids resemble the mature fossa of *Perotrochus* spp., but late in spermiogenesis, the solid rootlet and attached centrioles of *C. glyptus* become drawn into a greatly expanded fossa (Healy, 1989).

Incorporation of the future flagellar axoneme within the cytoplasm of spermatocytes and spermatids in *Perotrochus* warrants some comment. The same phenomenon can be seen in published micrographs of developing spermatids in the trochid *Monodonta turbinata* (Born, 1778) (see Kohnert & Storch, 1983) and in the turbinid *Lunella granulata* (see Koike, 1985). Unfortunately, neither Kohnert and Storch (1983) nor Koike (1985) offer a discussion of this positioning of the axoneme. In spermatids of the caudofoveate *Chaetoderma* sp., the proximal and distal centrioles each give rise to an axoneme within the cytoplasm (Buckland-Nicks & Chia, 1989). Of these two axonemes, only that associated with the future distal centriole survives into the mature spermatozoon. A similar situation has been reported by Eckelbarger *et al.* (1989) in paraspermatozoan development of the abyssal sea urchin *Phrissocystis multispina*, with the exception that both axonemes survive in the mature cell. Given the large number of abnormally developing spermatids observed in the ripe testes of our specimens of *Perotrochus quoyanus*, it cannot be ruled out that the intracellular axoneme in spermatids of this species may

material (sm) is thin. Arrowheads indicate axonemal profiles. **27.** Acrosomal vesicle showing granule cluster (g) and homogeneous portion (h) of vesicle contents. Note also subacrosomal material (sm). **28.** Granules (g) distributed in anterior and posterior depressions of homogeneous portion (h). Note ridged layer (rl) and basal rim defined by dense material (dm). **29.** Beginning of invagination (arrowhead) of homogeneous portion (h). **30.** Penetration of ridged layer (rl) into deepening invagination (arrowhead) of homogeneous portion. **31.** Acrosome of late spermatid showing developing basal invagination of acrosomal vesicle as well as invagination of homogeneous portion (arrowhead). Asterisk indicates electron-lucent plate. **32–34.** Sequence of ridged layer (rl) development shown in detail. Granule cluster (g). Asterisk indicates electron-lucent plate. **35.** Nearly mature acrosome. Electron-lucent plate indicated by asterisk. Subacrosomal material (sm). Scale bars: **25, 26** = 0.5 μ m; **27–35** = 0.25 μ m.

be an aberrant rather than normal feature. Examination of testes from animals collected at the commencement of the reproductive season should resolve this question.

Aberrations in spermatogenesis: Few ultrastructural studies have dealt with the incidence of spermatogenic abnormalities in mollusks. Takaichi (1979) detailed radiation-induced malformations of the mitochondrial sheath and nucleus and duplication of the axoneme in spermatids of the pulmonate *Euhadra hickonis*. Dorange and Le Pennec (1989) noted binuclear spermatids and angularly dislocated axonemes in late spermatids of *Pecten maximus* (Linné, 1758) and regarded these features as true aberrancies. O'Foighil (1985) suggested that angular dislocation of the axoneme in testicular sperm of the bivalve *Lasaea subviridis* Dall, 1899 could be due to slight immaturity. In *Perotrochus quoyanus* we have observed numerous spermatocytes and spermatids that were undergoing a form of development clearly different from normal spermatogenesis. Leaving aside the phenomenon of sperm dimorphism (a well-documented and 'normal' occurrence in many Caenogastropoda—see Healy, 1988a for discussion), the irregular shape of the condensed nucleus (pressed into shape by abutting cells), and the apparent inability of proacrosomal vesicles to fuse into a single acrosomal vesicle, strongly suggest that these are abnormal cells. Bearing in mind that a certain background level of spermatogenic abnormality probably exists in many if not most animal species (Bryan & Woloszewicz, 1973; Baccetti & Afzelius, 1976), we believe the appearance of aberrant cells in *P. quoyanus* is probably a normal event heralding the end of the annual reproductive phase in this species. We base this view on the fact that all three males examined were either spent or contained principally mature spermatozoa in the testis (with isolated pockets of developing and abnormal spermatogenic stages).

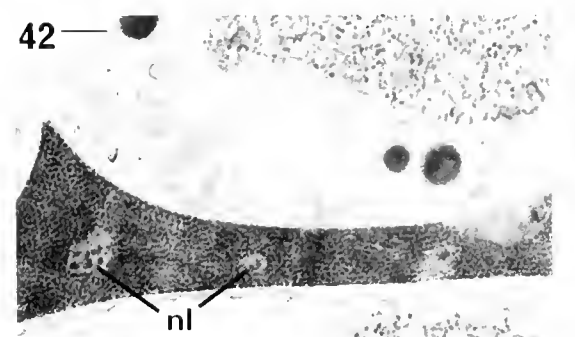
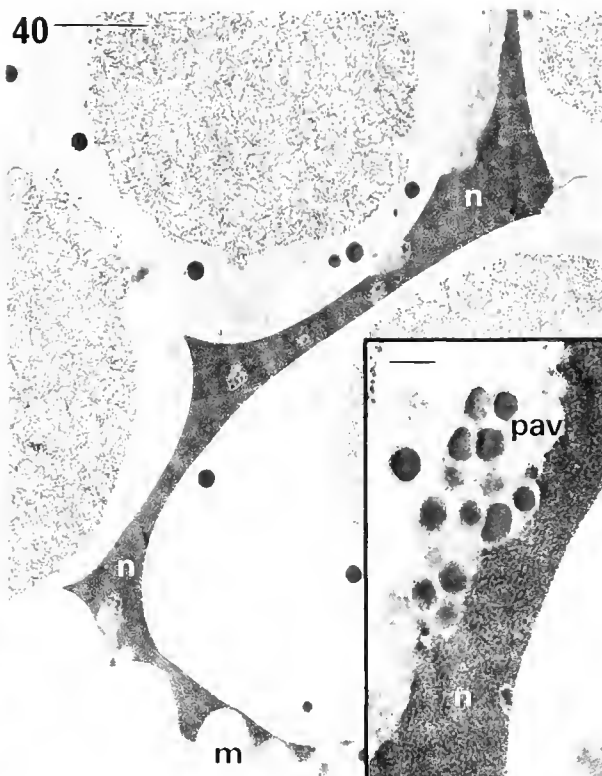
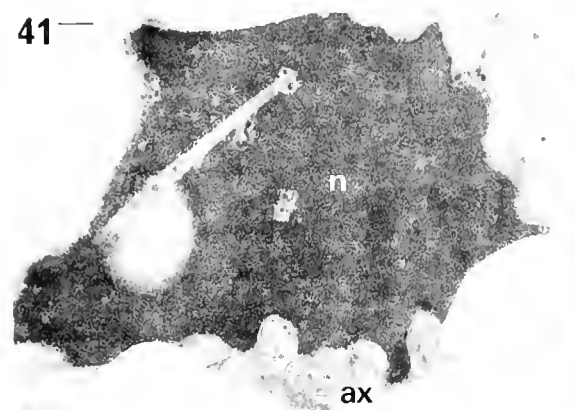
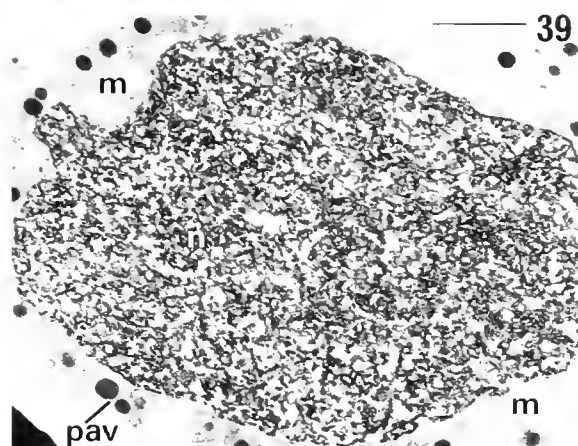
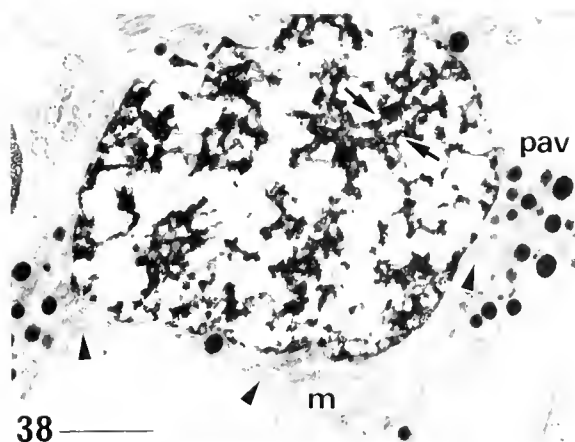
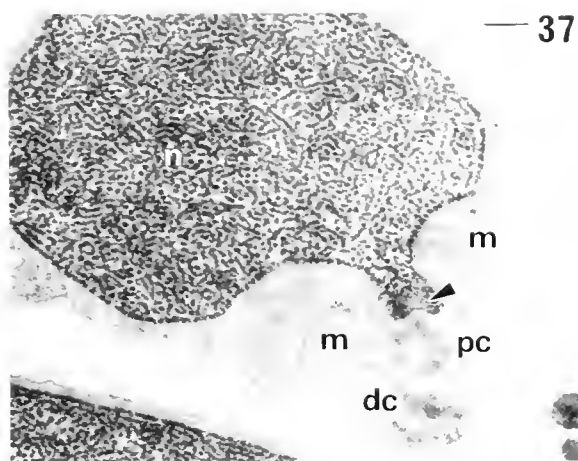
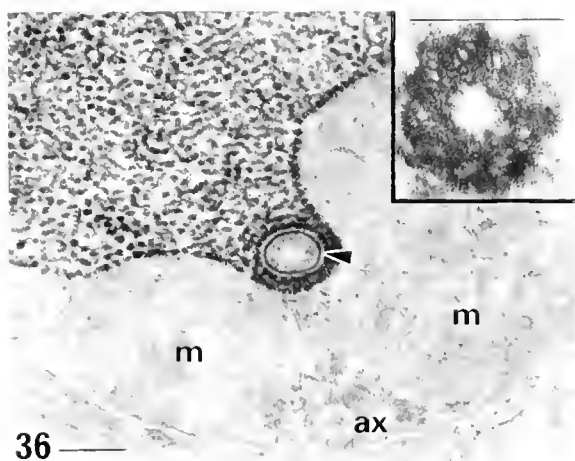
Spermatozoa: Healy (1988b) has previously drawn attention to the structural similarities between spermatozoa of *Perotrochus westralis* and those of the Trochoidea, particularly Trochidae. Our observations on glutaraldehyde-fixed testis sperm of *P. quoyanus* have enabled us not only to confirm these similarities but also to expand on details of the *Perotrochus* spermatozoon as reconstructed by Healy from sea-water formalin/ethanol-preserved material.

The electron-lucent anterior layer of the *Perotrochus* acrosomal vesicle contains regularly spaced ridges. Similar ridges have elsewhere been observed in the Trochi-

dae [*Austrocochlea constricta* (Lamarck, 1822), *Bankivia australis* (Menke, 1830); Healy & Daddow unpublished] and in the liotiid *Liotina peronii* (Kiener, 1839) (Healy & Ponder unpublished). It is interesting to note that the acrosomal vesicle of other pleurotomarioidean (*s.l.*) families (*Haliotis* spp.—Haliotidae, Lewis *et al.*, 1980; Sakai *et al.*, 1982; *Sinezona* sp.—Scissurellidae, Healy, 1990a) lack an electron-lucent anterior layer, whereas in the fissurellids *Scutus antipodes* Montfort, 1810 and *Montfortula conoidea* Reeve, 1842, a layer is present but exhibits no discernible ridged substructure (Healy, unpublished). The acrosomal complex in *Haliotis* and in *Sinezona* also differs from that of *Perotrochus* by having an extensive subacrosomal deposit similar to that seen in spermatozoa of some fissurellids (*Scutus antipodes*, *Montfortula conoidea*—see Healy, 1990a for illustrations) and many bivalve species (see references in Popham, 1979). The difference in appearance of subacrosomal material between *Perotrochus westralis* (rod-like) and *P. quoyanus* (diffuse, with some evidence of fibrous texture), may be due to use of different fixation methods (*P. westralis*—sea water formalin/ethanol; *P. quoyanus*—glutaraldehyde in cacodylate buffer). Azevedo *et al.* (1985) state that exposure of spermatozoa of *Gibbula umbilicalis* to sea water for five minutes resulted in a clearly defined rod (or perforatorium), derived from a formerly diffuse subacrosomal substance. It therefore seems possible that the subacrosomal rod of *P. westralis* may also be an end product of prolonged exposure to sea water. The dense layer of material visible within the subacrosomal material in the vicinity of the nuclear apex (see figs. 7, 8) may also be involved in rod formation. This layer was observed by Healy (1988b) in sea water-formalin/ethanol fixed sperm of *P. westralis* and interpreted as the possible remnants of nuclear membranes. Our observations, based on glutaraldehyde-fixed sperm of *P. quoyanus*, show that such material truly lies outside the intact nuclear and acrosomal membranes, and therefore constitutes part of the subacrosomal material.

The close resemblance of the crypt-like nuclear fossa of *Perotrochus* spp. (Healy, 1988b; this study) to the spermatid fossa of *Calliotropis glyptus* (Healy, 1989) has already been mentioned. In most vetigastropods and the Patellogastropoda, the centrioles are only superficially attached to a shallow nuclear invagination. In *Haliotis*, the proximal centriole itself sometimes occupies the shallow fossa (Lewis *et al.*, 1980; Sakai *et al.*, 1982), while in *Sinezona* (Scissurellidae) and *Calliotropis* (Trochidae) the centriole(s) and proximal portion of the axoneme are

Figures 36–42. *Perotrochus quoyanus*. 36,37. Developing nucleus (n), midpiece mitochondria (m), axoneme (ax), centriolar fossa (arrowhead), and proximal (pc) and distal centrioles (dc) of advanced spermatids. 36 Inset. Triplet microtubules of centriole in advanced spermatid. 38. Moribund spermatocyte showing synaptnemal complex (arrows), mitochondria (m), proacrosomal vesicles (pav) and axoneme profiles (arrowheads). 39. Aberrant spermatid. Note angular shape of cell and its condensing nucleus (n) as well as the presence of proacrosomal vesicles and mitochondria (m). 40. 'Mature' aberrant spermatozoon wedged between early (probably normal) spermatids. Note mitochondria (m) in depressions at base of nucleus (n). Inset. Detail of unfused proacrosomal vesicles (pav) from aberrant spermatozoon. 41. Fully 'condensed' nucleus (n) of aberrant sperm showing irregular shape and multiple axonemal profiles (ax). 42. Nuclear lacunae (nl) of aberrant spermatozoon. Scale bars. 36,37,40 Inset, 41, 42 = 0.25 μm ; 38–40 = 1 μm



actually contained within the fossa (Healy, 1989, 1990a). The ball-and-socket fitting of rootlet and centriolar fossa of *Perotrochus* spp. is unusual among gastropods, although a similar configuration occurs in the shipworm bivalve *Lyrodus bipartita* (Jeffreys, 1860) (see Figure 4 of Popham, 1974). Examination of other genera (*Mikadotrochus*, *Entemnotrochus*) may show this type of nuclear fossa to be a feature of all Pleurotomariidae.

Nuclear lacunae are widely reported in spermatozoa of externally fertilizing mollusks, polychaetes, brachiopods, echinoderms, as well as of some internally fertilizing groups (e.g. some teleosts, *Homo*) (Baccetti & Afzelius, 1976). Their occurrence or degree of development seems to be more closely linked with the mode of nuclear condensation than with the degree of modification of nuclear shape occurring during spermiogenesis. For example, in the trochoid *Zalipais laseroni*, the euspermatid nucleus undergoes marked elongation during condensation (fibro-granular pattern), but retains lacunae that ultimately fuse to form an axial tube within the mature, filiform nucleus (Healy, 1990b). Lacunae are usually not observed where nuclear condensation proceeds through either or both longitudinal fibrillar and lamellar phases (see Kaye, 1969; Horstman, 1970; Maxwell, 1983; Kohner & Storch, 1984b; Koike, 1985).

The midpiece and satellite fiber/centriole complex of *Perotrochus* spp. are essentially as observed in the majority of Vetigastropoda and Patelloidea (Koike, 1985; Hodgson & Bernard, 1988; Healy, 1990a; Healy & Daddow unpublished), the Bivalvia (for references see Popham, 1979), Scaphopoda (Dufresne-Dube *et al.*, 1983) and Caudofoveata (Buckland-Nicks & Chia, 1989). The same arrangement of these organelles, clearly one associated with sperm tail attachment and stability, also occurs in spermatozoa of many other externally fertilizing animal species (for major references see Baccetti & Afzelius, 1976; Wirth, 1984).

The flagellum consists of an axoneme (9+2 microtubular substructure) sheathed by the plasma membrane. Our scanning electron micrographs reveal that the flagellum is narrower in diameter close to the nucleus. TEM observations suggest that this is probably the result of a more closely applied plasma membrane in this region of the flagellum, although slight narrowing of the axoneme does occur near the distal centriole (see figs. 4, 15). At present we cannot clarify the origin of the dense body sometimes observed within the flagellum (see fig. 17). It was not observed in longitudinal sections through the immediate post-nuclear region of the flagellum and could yet prove to be an artifact of fixation.

Systematic Considerations: If spermatozoa of *Perotrochus* spp. are representative of the Pleurotomariidae, then a closer relationship between this family and the Trochoidea (particularly Trochidae) than with the other pleurotomarioidean (*s.l.*) families Haliotidae and Scissurellidae seems evident. This conclusion accords both with Haszprunar's (1988, 1989) finding that no synapomorphies exist to unite the Pleurotomarioidea (*s.l.*), and with his decision to place the Haliotidae and Scissurel-

lidae into separate superfamilies within the Vetigastropoda. The question as to whether ancestral vetigastropods were more like scissurellids than pleurotomariids (see Haszprunar, 1988, 1989 for discussion) cannot yet be resolved using sperm data alone because too many significant taxa (including the new hydrothermal vent groups) remain unstudied. Based on the present evidence, however, we suspect that spermatozoa of any stem vetigastropod would have resembled more closely the unmodified type of *Perotrochus* (Healy, 1988b; this paper) than the modified type of *Sinezona* (Healy, 1990a).

Vetigastropoda, Patellogastropoda and Neritimorpha can be distinguished on the basis of sperm features (especially acrosomal and nuclear) and features of spermiogenesis (dimorphic in the case of the Neritimorpha; rarely so in the Vetigastropoda) (Koike, 1985; Healy, 1988a, 1990a,b). It will be interesting to determine whether the cocculinids—once included in the Vetigastropoda (Salvini-Plawen, 1980) but since removed to a separate archaeogastropod suborder, Cocculiniformia (Salvini-Plawen & Haszprunar, 1987)—also show characteristic sperm and spermiogenic features.

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Tenagodus or *Siliquaria*? Unraveling Taxonomic Confusion in Marine “Worm-Snails” (Cerithioidea: Siliquariidae)

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ABSTRACT

The nomenclatural history and availability of some genus- and family-group names in the marine “worm-snail” family Siliquariidae are discussed. (1) *Tenagodus* Guettard, 1770 (type species, *Serpula anguina* Linné, 1758) has priority over its objective junior synonym *Siliquaria* Brugnière, 1789. *Tenagodes*, *Tenagoda* and *Silicaria* are unjustified emendations. *Siliquaria* Schumacher, 1817 (also subsequently emended to *Silicaria*) is a junior homonym described in the Bivalvia. (2) *Siliquarius* Montfort, 1810 (type species *Siliquarius anguilus* Montfort, 1810) is an available name. (3) *Anguinaria* Schumacher, 1817, is preoccupied by *Anguinaria* Lamarck, 1816 (Bryozoa). (4) *Montfortia* Della Campana, 1890 (non *Montfortia* Récluz, 1843), and its replacement name *Hemitenagodus* Rovereto, 1899, are based on the type species *Tenagodus bernardii* Mörch, 1860. (5) *Agathirsus* Montfort, 1808, is based, by original designation, on the type species *Agathirsus furcellus* Montfort, 1808 (a senior synonym of *Siliquaria spinosa* Lamarck, 1818). *Agathysus* Herrmannsen, 1846, is an unjustified emendation. “Agathinus,” “Agathirsis” and “Agathirsus” are incorrect subsequent spellings. (6) The family name Siliquariidae Anton, 1838, has priority over its objective junior synonym Tenagodidae Gill, 1871.

Key words: Taxonomy, Nomenclature, Synonymy, Gastropoda.

INTRODUCTION

Marine “worm-snails” are now understood to be members of three different families, the Vermetidae, genus *Vermicularia* in the Turritellidae, and Siliquariidae (e.g., Morton, 1951, 1953; Bieler, 1990). The siliquariids, often (but not always) recognizable by longitudinal shell slits or series of holes, are an enigmatic group. Little is known about their biology and geographical distribution, and the published literature provides seldom more than descriptions of empty shells or shell fragments. Considerable confusion exists about the synonymy and relationships of nominal taxa such as *Tenagodus* and *Siliquaria*, or Tenagodidae and Siliquariidae. In the aftermath of more than 200 years of misspelling, emending and re-

placing certain names, today’s worker is left to wonder about how many “real” taxa are hidden behind *Tenagodus*-*Tenagodes*-*Tenagoda*, *Siliquaria*-*Silicaria*-*Siliquarius*, or *Agathirsus*-*Agathysus*-*Agathinus*. This is complicated further by family names that were later based on some of these names.

This paper will not discuss phylogenetic relationships, a topic that demands detailed anatomical studies that are in progress (Bieler, in preparation). No interpretation of subjective synonymy between nominal genera in the Siliquariidae will be made before that study is complete. However, taxonomic problems often can be solved by a careful study of existing literature and application of ICZN rules. This contribution is meant as a taxonomic “house cleaning,” addressing problems of type species, priority and availability of various generic and family names for this group. A main goal is to identify objective synonymies (and consequently reduce the number of nominal taxa in future publications).

TAXONOMY

Genus-group names

Tenagodus Guettard, 1770

Type species: *Serpula anguina* Linné, 1758.

The name *Tenagodus* was first made available by Guettard (1770:128). Several later authors (e.g., Herrmannsen, 1849:540; Della Campana, 1890:139; Cossmann, 1912:146) refer to an earlier work by Guettard (usually cited as “1760”) for the introduction of *Tenagodus* or “*Tenagoda*.” However, that publication, “Année 1760” of the *Histoire de l’Académie Royale des Sciences* (1766a, b), contains only vernacular names in text and figure captions. Guettard (1770) did not indicate a type species. The first subsequent designation of a type species appears to be that of Adams and Adams (1854:360–361), who selected “[*Tenagoda*]. *anguina*, Linnaeus” [*Serpula anguina* Linné, 1758].

Two different emendations of *Tenagodus* (unjustified in the sense of ICZN Art. 33) were introduced:

Tenagodes P. Fischer, 1885 (p. 692); Sacco, 1896:17; Cossmann, 1912:146.

Tenagoda Agassiz, 1848 (p. 1049); Herrmannsen, 1849:540; Adams & Adams, 1854:360, corrected to *Tenagodus* in 1858:656; Chenu, 1859:321; Paetel, 1869:9.

Siliquaria was first introduced by Bruguière (1789:xv). The type species is *Serpula anguina* Linné, 1758, by subsequent monotypy (Lamarck, 1799:79). Bruguière's *Siliquaria* was later erroneously credited to Lamarck (e.g., Schumacher, 1817:262; Rang, 1829:187). *Silicaria*, an emendation of *Siliquaria* Bruguière or "Lamarck" (unjustified in the sense of ICZN Art. 33), was introduced and used by some authors (e.g., Bosc, 1802:157; Daudin, 1800:32; Audouin, 1829b).

Siliquaria was also described as a genus of bivalves, by Schumacher (1817:43, 129). Schumacher knew of the conflict with the earlier name, and conserved his nominal taxon by dismissing the senior homonym. For the latter he introduced the new worm-snail genus *Anguinaria* (see below): "Je n'ai pu conserver le nom de ce genre donné par Mr. Delamarck savoir: Silicaire (Silicaria), comme il y a un genre parmi les bivalves qui porte un nom presque semblable" (1817:262). *Siliquaria* Schumacher was also subsequently emended to *Silicaria* (e.g., Paetel, 1875:191).

Discussion of the type species

Linné's (1758:787) *Serpula anguina* was originally based on more than one species, and the Linnean collection contains specimens of several forms, with no clear type specimen indicated (Hanley, 1855:448). Linné had adopted the species name from the non-binominal "Solen anguinus" of Rumphius (1705:125) and referred to figures in that work (Rumphius, 1705: pl. 41, fig. H) and in Argenville (1742: pl. 29, fig. 11). Rumphius' figure shows a spiny specimen of *Tenagodus*; Argenville's illustration is that of a member of the Vermetidae and was later used by Linné (1767:1266) as reference to *Serpula arenaria* Linné, 1758. The type locality for *S. anguina* was given as "India" (Linné, 1758:788). Linné also listed several references to a variety "β" (e.g., Rumphius, 1705: pl. 41, fig. 2; Gualtieri, 1742: pl. 10, fig. Z). Most of these latter illustrations show a spineless Mediterranean form of *Tenagodus* later described as *Anguinaria obtusa* Schumacher, 1817 (see below).

Born (1780:440), possibly misled by Linné's statement in the *Museum Ulricae* (1764:701) that the variety had a spiny shell, then confused the issue by applying the name *Serpula anguina* to the smooth form and introducing the name *Serpula muricata* for the true *anguina*. Lamarck (1801:98) based his interpretation of *S. anguina* on yet another illustration of a smooth form, by Davila (1767: pl. 4, fig. E), later described as *Siliquarius anguilus* Montfort, 1810 (see below). Many subsequent authors (e.g., Lamarck, 1818:337; Philippi, 1836:173; Chenu,

1843:1; Cossmann, 1912:146) followed and sometimes defended (Weinkauff, 1868:330) Born's misconception. Although the problem was discussed at several occasions [Hanley, 1855:448; Mörch, 1860b:403; Tryon, 1886:189; Sowerby, 1876:(1)], the name *anguina* remained mistakenly in use also for the smooth Mediterranean form, especially in paleontological works (e.g., Strausz, 1966:122).

When Lamarck (1799:78) and Adams & Adams (1854:361) employed the name *anguina* in fixing the type species of *Siliquaria* and *Tenagodus*, respectively, it was in this misidentified fashion. Lamarck (1799:78–79) mentioned a shell without spines for *Siliquaria*, and his later works (e.g., 1801, 1818) clearly identify the Mediterranean form. Adams and Adams (1854:361) mentioned that the "typical species is found in the Mediterranean" and their illustrations in the same work (pl. 39, fig. 5) show smooth Mediterranean specimens.

To best serve stability in nomenclature, and in agreement with current usage (e.g., Wenz, 1939:679; Malatesta, 1974:200; Squires, 1990:286), the nominal species named in fixation are here accepted as type species, regardless of misidentification. A referral to the International Commission on Zoological Nomenclature, as specified in ICZN Article 70(b), seems unnecessary in this case.

The synonymy of *Tenagodus* and *Siliquaria* has long been known (e.g., Chenu, 1843:1; Herrmannsen, 1849:540; Paetel, 1869:xiii, 56; Keferstein, 1862–66:1056), and the priority of *Tenagodus* was stressed by some authors (e.g., Strausz, 1966:122). Other workers, however, rejected *Tenagodus* as non-binominal (e.g., Dall, 1889:259; Gould, 1966:3; Abbott, 1974:96), and both names have been used in parallel for the past 200 years.

The genus-group name *Tenagodus* is available and has priority over *Siliquaria* (a junior objective synonym), for reasons given below:

- (1) The name *Tenagodus* was used as a scientific name by the author when published [ICZN Art. 11(b)]. Guettard's description (1770:128) begins "Genre X. *Tenagodus*, Tenagode [the French vernacular]. Caractere générique. . ."
- (2) The name *Tenagodus* was introduced in a work published before 1931 and containing uninominal genus-group names without associated nominal species. It can be accepted "as consistent with the Principle of Binominal Nomenclature in the absence of evidence to the contrary" [ICZN Art. 11(c)(i)].
- (3) The original work contains a description, illustrations, and bibliographic references to additional illustrations, thus fully satisfying ICZN Art. 12 (a new scientific name published before 1931 must have been accompanied by a description, definition or indication).
- (4) The work has not been placed on the Official Index of Rejected and Invalid Works [ICZN Art. 78(h)].
- (5) Other genus-group names introduced in the same work in similar fashion are in current use, such as

Kuphus, *Uperotus* and *Brechites*, which were accepted by later workers (e.g., Turner, 1966; Smith, 1971) for same reasons. A suppression of Guettard's work by plenary power of ICZN would create new taxonomic problems.

- (6) The name *Tenagodus* (in various spellings) has been used frequently (e.g., Mörch, 1860a, b; Fischer, 1885; Sacco, 1896; Martin, 1899; Simroth, 1906; Cossmann, 1912; Thiele, 1929; Wenz, 1939; Strausz, 1966; Malatesta, 1974; Boss, 1982). It does not qualify as an "unused senior synonym" [ICZN Art. 79(c)].
- (7) *Siliquaria* Bruguière, 1789, and *Tenagodus* Guettard, 1770, have (by subsequent designations) the same type species; they are objective synonyms.

***Siliquarius* Montfort, 1810**

Type species: *Siliquarius anguillus* Montfort, 1810.

Siliquarius was introduced by Montfort (1810:39). The type species, by original designation, was given as *Siliquarius anguillus* (Montfort, 1810). The description was accompanied by a drawing of a siliquariid shell without spines, and Montfort made reference to a figure by Davila (1767: pl. 4, fig. E) and to *Siliquaria anguina sensu* Lamarck, 1801 (who had based his concept of *S. anguina* on Davila's figure).

Siliquarius was used by some later authors (e.g., Mörch, 1860b) because *Siliquaria* was considered "preoccupied" for a genus of plants by Forskål (1775). The name *Siliquarius* Montfort is available for nomenclatural purposes.

***Anguinaria* Schumacher, 1817**

[preoccupied]

Schumacher (1817:262) introduced *Anguinaria* and included two new species: *Anguinaria obtusa*, referring to "*Serpula anguinaria* [err. pro *anguina*]" *sensu* Born (1780:440, pl. 18, fig. 15), and *Anguinaria rubra*, referring to *Serpula anguina*, *sensu* Martini (1769:50, pl. 2, figs. 13–14). No subsequent type species designation was located.

The name *Anguinaria* Schumacher, 1817, is not available for nomenclatural purposes, because it is preoccupied by *Anguinaria* Lamarck, 1816 (p. 142; Bryozoa).

***Hemitenagodus* Rovereto, 1899**

Type species: *Tenagodus bernardii* Mörch, 1860.

Della Campana (1890:139–140) introduced the genus-group name *Montfortia* as a subgenus of *Tenagodus* (p. 139) or new genus (p. 140). The name *Montfortia* was based, by original designation, on *Tenagodus* (*Siliquarius*) *bernardii* Mörch, 1860 (1860a:368, a sponge-dwelling Recent form from unknown type locality). Later workers (e.g., Wenz, 1939:680) erroneously considered the fossil species *Montfortia ligustica* Della Campana, 1890, as type species by monotypy.

Rovereto (1899:108) recognized *Montfortia* Della Campana, 1890, as preoccupied by *Montfortia* Récluz, 1843, and introduced the replacement name *Hemitenagodus*.

Thus, *Hemitenagodus* is also based on *Tenagodus bernardii* Mörch.

***Agathirses* Montfort, 1808**

Type species: *Agathirses furcellus* Montfort, 1808.

Montfort (1808:399) introduced *Agathirses* with *A. furcellus* as type species by original designation ("Espèce servant de type au genre") for an Eocene fossil. The species name was borrowed from "furcelle (furcella)," listed as a "singulier tube testacée multioculaire" of uncertain systematic placement by Lamarck (1801:104). Montfort referred to the "Siliquaire de Grignon" as illustrated by Faujas-St.-Fond (1803: pl. 3). Lamarck (1818: 338) eventually also named the Grignon fossil, as *Siliquaria spinosa*. Sherborn (1930:6087) erred when he credited the name *Siliquaria spinosa* to G. Fischer (1807: 244), who had only used the French vernacular "Siliquaire épineuse." Later authors erroneously cited the junior synonym, *Siliquaria spinosa* Lamarck, as type species of *Agathirses* (e.g., Herrmannsen, 1846:25; Cossmann, 1912:148; Wenz, 1939:680).

At least one intentional emendation of *Agathirses* (unjustified in the sense of ICZN Art. 33) was introduced:

Agathysus Herrmannsen, 1846 (p. 25), Agassiz (1848:29); Cossmann, 1912:148

"Agathinus Mft." Paetel (1888:499), "Agathirsis Mft." Paetel (1875:5) and "Agathirsus Cossmann, 1912" Wenz (1939:680) are here considered incorrect subsequent spellings without nomenclatural bearing [ICZN Art. 33(c)].

Family-group names

Siliquariidae

[based on *Siliquaria* Bruguière, 1789]

Siliquariidae was first introduced by Anton (1838:xiii), as "Siliquariacea." The name was frequently credited to later authors, such as Chenu, 1859; it was also independently proposed by several later workers (e.g., Morton, 1951:40) unaware of its earlier introduction. This is Siliquariadae Schaufuss in Paetel (1869:9) and "Siliquariidae" auct. (e.g., Paetel, 1869:9).

Tenagodidae

[based on *Tenagodus* Guettard, 1770]

Tenagodidae was first proposed by Gill (1871:8). It was also independently introduced by later authors who overlooked the earlier introduction (e.g., Malatesta, 1974: 200).

Although the genus-group name *Tenagodus* has priority over *Siliquaria*, the family-group name Siliquariidae has priority over Tenagodidae:

- (1) Both generic names have been the basis of family names.
- (2) The family-group names Siliquariidae and Tenagodidae are objective synonyms, because their name-

bearing genera are objective synonyms [ICZN Art. 61(c)(ii)].

- (3) As the senior synonym, Siliquariidae can continue in use although *Siliquaria* is a junior synonym, because the Principle of Priority also applies to family-group names concerned [ICZN Art. 40(a)(i)].

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Nucella Röding, 1798 (Gastropoda: Muricidae): Type Species

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ABSTRACT

Buccinum filiosum Gmelin, 1791 [junior synonym, *Nucella theobroma* Röding, 1798, senior synonym *Buccinum lapillus* Linnaeus, 1758; now known as *Nucella lapillus* (Linnaeus)], is the type species of *Nucella* Röding 1798 by subsequent designation of Stewart (1927:386, footnote #260).

Key words *Nucella lapillus*, type species, taxonomy, Muricidae

INTRODUCTION

Röding (1798:130–131) introduced the genus *Nucella* and included five names: *N. reticulata*; *N. moschatellina* with *Buccinum laeve* Gmelin, 1791 listed as a synonym; *N. macina*; *N. lapillus* with *Buccinum rusticum* Gmelin, 1791 as a synonym; and *N. theobroma* with *Buccinum filiosum* Gmelin, 1791 as a synonym. Röding did not specify a type species. Because the type species was not fixed in the original publication, only the subsequent designation of a type species from the nomina enumerated above is valid in accordance with Article 69 (Code of the International Commission on Zoological Nomenclature [hereafter I.C.Z.N.] (1985)). Several authors have either incorrectly designated a type species for *Nucella* or discussed efforts to designate a type. This confusion was partly caused by the fact that the binomen *Nucella lapillus* Röding is a secondary homonym, but not a synonym, of *Buccinum lapillus* Linnaeus, 1758.

TAXONOMIC HISTORY: A COMEDY OF ERRORS

Dall (1906; 1909), Clench (1947), and, in more detail, Rehder (1962) discussed the species introduced by Röding (1798) in *Nucella*. The first species, *N. reticulata*, is the cancellariid *Cancellaria reticulata* (Linnaeus, 1767); the second, *N. moschatellina* is a *nomen dubium*; the third, *N. macina* is a *nomen nudum*; the fourth, *N. lapillus*, not to be confused with and not the same as *Buccinum lapillus* Linnaeus, 1758, had in its synonymy *Buccinum rusticum* Gmelin, 1791 and is identified as *Latirolagena smaragdula* (Linnaeus, 1758); the fifth species, *Nucella theobroma*, with *Buccinum filiosum* Gme-

lin, 1791 listed as a synonym, is a subjective junior synonym of *Buccinum lapillus* Linnaeus, 1758, now referred to as *Nucella lapillus* (Linnaeus, 1758) (Kool, 1989).

Dall (1906), after prompting acceptance of Röding's names, acknowledged that determining the correct type species for *Nucella* would "require special study to unravel." In a later work, Dall (1909) provided not one, but three different binomina for the type species designation, without mentioning the word "type."

First, in his list of subgenera within the genus *Thais*, he (1909:46–47) cited "*Purpura filiosa* Menke = *P. lapillus* L." after *Nucella*. Wenz (1941:1123) mistakenly interpreted this as a species designation and credited Dall (1909) with the designation of "*N. filiosa* (Gmelin) [*Buccinum*] = *lapillus* (Linné) [*Buccinum*]." Whatever the inappropriateness of this invalid designation, Dall left no doubt that he recognized these specific nomina as synonyms by placing "*P. lapillus* L." in synonymy with *Purpura filiosa* "Menke" [= *Buccinum filiosum* Gmelin]. It should be mentioned that Dall's attribution of *filiosa* to Menke (1830:62) was an erroneous concession to the custom of the nineteenth century where some authors credited themselves for a specific name after having altered the generic placement and, thus, the binominal combination, in this case, from *Buccinum filiosum* to *Purpura filiosa*.

Secondly, in the same work, Dall (1909:48) stated "... thus fixing the name *Nucella* on the well-known *Purpura lapillus*, ...," by which action he obviously meant to restrict, by subsequent designation, the concept of *Nucella*, but he again did not mention the necessary word "type."

Thirdly, in another listing of subgeneric and sectional taxa, Dall (1909:50) designated many type species, and he placed "*T. lapillus* (Linn)" right after *Nucella s.s.*, probably meaning this to be a type designation. But although *Nucella* is on that list, he again failed to use the word "type." Therefore, whatever his intentions, Dall (1909) provided three different, ambiguous, indefinite and invalid subsequent designations.

Later works that treated *Nucella* include Suter (1913:425), who listed "*Purpura lapillus* L." as type species of *Nucella*, an invalid designation, because *lapillus* Lin-

naeus was not included among the species of *Nucella* in Röding (1798), and is therefore not available (I.C.Z.N., Article 69).

Iredale (1915:472), without realizing that Dall had not designated a valid type species for *Nucella*, reprinted Dall's (1909:50) list and added the word "Type," but misquoted Dall by listing "*T. lapillus* Lam." instead of "*T. lapillus* (Linné)."

Dall (1915:557) discussed the type species designation of *Nucella* and stated: "The type of the subgenus is the solitary North Atlantic species of *N. lapillus* of Linnaeus, . . ." However, although Dall mentioned the word "type," *lapillus* Linnaeus is not available because it was not a name included under *Nucella* by Röding (1798).

Stewart (1927:386) wrote in a footnote (#260): "[*Nucella*:] Type species *Buccinum filosum* Gmelin = *B. lapillus* L." Stewart was the first author to designate a valid type species for *Nucella*, without realizing this himself; he continued: "It is probably safe to say that Dall fixed the type in 1909." The species *Buccinum filosum*, originally used by Röding [as a synonym of *Nucella theobroma* Röding] in *Nucella*, is nomenclatorially available for the type designation. Stewart also recognized that *B. filosum* was synonymous with *B. lapillus* Linnaeus.

Treating *Nucella* as a separate genus with four sections, Thiele (1929:298) mentioned *Nucella* (*Nucella*) *lapillus* (Linné) as an example; he did not, however, use the word "type," and none of the available nomina was cited.

Grant and Gale (1931:716), following Stewart (1927), also credited Dall (1909) as the subsequent designator and gave the type as "*Nucella lapillus* Linnaeus." However, aside from not being available, this binomen was not one of the three combinations cited by Dall as possible types.

In his list of the type species of marine mollusca of the British Isles, Winckworth (1932:229) listed *N. theobroma* Röding, 1798 as the "genotype" of *Nucella*; however, Stewart's (1927) type designation preceded this one.

Winckworth (1945:141), as he had done in his 1932 paper, again cited *N. theobroma* Röding as type species of *Nucella* and correctly noted that it was a junior synonym of *Buccinum lapillus* Linnaeus. However, he erroneously attributed the designation to Dall (1909), who never used the name *theobroma*.

Clench (1947:86) in an ambiguous treatment of *lapillus* Linnaeus, placed the species in the genus *Thais* (Röding, 1798) and used the subgeneric name *Polytropa* Swainson, 1840 [type species *Buccinum lapillus* Linnaeus by subsequent designation, J.E. Gray, 1847], rather than *Nucella*. Clench's argument for not using *Nucella* was that Röding never intended to include *Buccinum lapillus* Linnaeus in his genus *Nucella*. Clench arrived at this conclusion after comparing the figures in Martini (1777: pl. 121, figs. 1111–1112) for *lapillus* Linnaeus and those for *filosum* Gmelin (pl. 121, figs. 1113–1114). According to Clench, the figures for Röding's *Nucella theobroma* and its synonym *Buccinum filosum* Gmelin, are unrecognizable, whereas the figures of Röding's *Nassa rudis*

and its associated synonym, "*Buccinum lapillus* Gmelin," are those of *Buccinum lapillus* Linnaeus. The latter portion of this argument is true, but the former, as Rehder (1962) pointed out, is not tenable: the "unrecognizable" figures of *Nucella theobroma* in Martini (1777: pl. 121, figs. 1113–1114) also clearly represent *Nucella lapillus* Linnaeus, in one of its many variations. Rehder (1962, figs. 1–2) illustrated a specimen of *lapillus* from France that closely matched Martini's (1777: pl. 121, figs. 1113–1114) illustrations. It has long been known that the species displays a high degree of variation in shell morphology and color (Martini, 1780: pl. 122, figs. 1124–1125, 1128–1129; Forbes & Hanley, 1851; Crothers, 1985). In his discussion of *Nucella*, Clench did not mention the attempted designations of Dall (1915), Suter (1913), Winckworth (1932), and the valid designation of Stewart (1927).

Clench's usage of *Polytropa* instead of *Nucella* is not followed herein. *Nucella* is a valid taxon to be used for Linnaeus' *lapillus*. Interestingly enough, Clench cited "*Purpura filosa* Menke" and "*Buccinum filosum* Gmelin" in his synonymy of "*Thais* (*Polytropa*) *lapillus* Linné," which contradicts his own argument that Röding never intended to include *Buccinum lapillus* Linnaeus in his genus *Nucella*.

Finally, in an attempt to resolve some of the irregularities and inconsistencies discussed so far, Rehder (1962: 110) stated that Dall (1909:50) intended to designate a type and that another possible attempt at a designation (Dall, 1909:46) is invalid because Dall cited *filosa* Menke, not *filosa* Gmelin. Further, Rehder attributed the earliest type designation to Winckworth (1932:229) who listed *Nucella theobroma* and pointed out that Clench (1947) had overlooked this type designation.

SUMMARY

In conclusion, the correct type species for *Nucella* Röding, 1798 is *Buccinum filosum* Gmelin, 1791, a subjective junior synonym of *Buccinum lapillus* Linnaeus, 1758, and an objective senior synonym of *Nucella theobroma* Röding, 1798, by subsequent designation of Stewart (1927: 386, footnote #260).

ACKNOWLEDGMENTS

The authors thank Mr. Richard L. Johnson for a critical review of an earlier draft of this paper, and are indebted to two anonymous reviewers.

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A Revision of the Recent Species of *Eudolium* Dall, 1889 (Gastropoda: Tonnoidea)

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ABSTRACT

The tonnid genus *Eudolium* contains three Recent species: *E. crosscanum* Monterosato, 1869 (= *thompsoni* McGinty, 1955), *E. bairdii* Verrill & Smith (= *solidior* Dautzenberg & Fischer, 1906 = *lineata* Schepman, 1909 = *inflatum* Kuroda & Habe, 1952 = *kuroharai* Azuma, 1960) and *E. pyriforme* Sowerby, 1914. *Eudolium crosscanum* and *E. pyriforme* respectively have amphiatlantic-Mediterranean and Indo-Pacific distributions, while *E. bairdii* occurs widely in the Atlantic, Pacific and Indian Oceans. Genus and species group synonymies and distributions are discussed, and shells, radulae and male external anatomies are illustrated.

Key words: Mollusca; prosobranch gastropods; Tonnidae; *Eudolium*; systematics; zoogeography

INTRODUCTION

The taxonomy of the species of the prosobranch family Tonnidae is poorly understood. Atlantic species were revised by Turner (1948), but there has been no critical modern revision of the Indo-Pacific species. The present contribution is the result of an attempt to determine the identity of two species of the genus *Eudolium* Dall, 1889 obtained off New Zealand in recent years.

Since Dall's (1889a) review, *Eudolium bairdii* (Verrill & Smith, 1881) has been treated as a synonym of *E. crosscanum* (Monterosato, 1869) by the majority of authors. From examination of numerous specimens, however, it transpires that not only are they distinct species, but that five subsequently introduced taxa are synonyms. Moreover, *E. crosscanum* is more closely related to the Indo-Pacific *E. pyriforme* (Sowerby, 1914) than to *E. bairdii*.

ABBREVIATIONS AND TEXT CONVENTIONS

AMS—Australian Museum, Sydney.
MCZ—Museum of Comparative Zoology, Harvard.
MNHN—Muséum National d'Histoire Naturelle, Paris.
NMNZ—National Museum of New Zealand, Wellington.
NMP—Natal Museum, Pietermaritzburg.
USNM—National Museum of Natural History, Washington, DC.

In captions to illustrations shell height dimension precedes diameter.

SYSTEMATICS

Class Gastropoda

Superfamily Tonnoidea Suter, 1913

Family Tonnidae Suter, 1913

Genus *Eudolium* Dall, 1889

Doliopsis Monterosato, 1872(not Vogt, 1852, nor Conrad, 1865):

5. Type species (by monotypy): *Dolium crosscanum* Monterosato, 1869, Recent, Mediterranean

Eudolium Dall, 1889a:232. Substitute name for *Doliopsis* Monterosato (preoccupied).

Galeodolium Sacco, 1891:4. Type species (by subsequent designation of Vokes, 1986:178): *Cassidaria mutica* Michelotti, 1861; Oligocene, Italy.

?*Tuberculodolium* Sacco, 1891:9. Type species (by subsequent designation of Vokes, 1986:178): *Eudolium antiquum* Sacco, 1890; Oligocene, Italy.

?*Simplicodolium* Sacco, 1891:13. Type species (here designated): *Pyrula fasciata* Borson, 1821; Pliocene, Italy.

Remarks: The shells of *Eudolium* species differ from those of *Tonna* Brunich, 1771 in having more narrowly tapered bases, consistently narrow, widely spaced spiral cords with narrow secondary spirals, and fine axial sculpture on all teleoconch whorls. The two groups are certainly closely related, with similar shells, radulae, jaws and external anatomies. An operculum is lacking in both groups, at least in the adults. *Eudolium* species are most commonly encountered at 200–600 m depth, while few *Tonna* species range much deeper than 50 m. Although *Eudolium* has been placed as a subgenus of *Tonna* by some authors (e.g., Dall, 1889a,b; Vredenburg, 1919; Thiele, 1929; Kilius, 1962), I prefer to treat it at generic level because of the distinctive shell facies and deeper center of bathymetric distribution.

As here interpreted the genus *Eudolium* contains three Recent species: *E. crosscanum* (Monterosato, 1869), *E. bairdii* (Verrill & Smith, 1881), and *E. pyriforme* (Sowerby, 1914). Of other species that have been referred

here. *Dolium* (*Eudolium*) *verrilli* Dall, 1889 has been transferred to *Hadroocorys* Quinn, 1950 (Quinn, 1950), while *E. aulacodes* Tomlin, 1927 belongs in *Oocorys* Fischer, 1883 (Kilburn, 1956). *Parvitonna perselecta* Iredale, 1931 was referred to *Eudolium* by Kilias (1962), but the holotype (AMS C.57790) is clearly a species of *Tonna* (*sensu stricto*). *Tonna tessellatum* (Bruguière, 1759), *T. fasciatum* Bruguière, 1759 and *T. zonatum* (Green, 1830) were referred to *Tonna* (*Eudolium*) by Vredenburg (1919), but they too belong in *Tonna* (*sensu stricto*).

Vokes (1956) interpreted Cossmann's (1903:139) statement "types de *Galeodolium* et de *Tuberculodolium*: *E. antiquum* Sacco, *Cassid. mutica* Michelotti, d'après les types communiqués par M. Sacco" as the first valid subsequent designation of type species for *Galeodolium* and *Tuberculodolium*. Cossmann, however, inadvertently reversed the order of the "type" species and thus selected species that were not originally included (ICZN Art. 69a). Although Vokes simply corrected the order, Cossmann must be considered to have associated the names *respectively*, so it is concluded that Cossmann's selection is invalid. Accordingly, Vokes (1956) is considered to be the first subsequent designator of the type species of these taxa.

Vokes (1956) used *Galeodolium* as a subgenus of *Eudolium* for species with strong nodules and a reflexed, denticulate outer lip. The differences between the type species of *Eudolium* and *Galeodolium* (Michelotti, 1861: pl. 13, fig. 16; Sacco, 1891: pl. 1, fig. 1), however, are simply matters of degree, because *E. bairdii* exhibits a smooth morphological transition between the extremes in its infraspecific variability (see below). Placement of *Tuberculodolium* and *Simpliciodolium* in synonymy is tentative pending study of the type material, which was not available to me. Judging from published photographs, the undoubtedly juvenile holotype of *Eudolium antiquum* Sacco, 1890 (Ferrero Mortara *et al.*, 1984) seems narrower than confirmed species of *Eudolium*, while the lectotype of *Pyrula fasciata* Borson, 1821 (Pavia, 1976) may be a juvenile *Tonna*. Because *Galeodolium* and *Eudolium* are regarded as synonyms, and as *Eudolium* and *Tonna* are undoubtedly confamilial, Ga-

leodoliidae Sacco, 1891 is treated as a synonym of Tonnidae Suter, 1913 (1825). Tonnidae is conserved using ICZN Art. 40b.

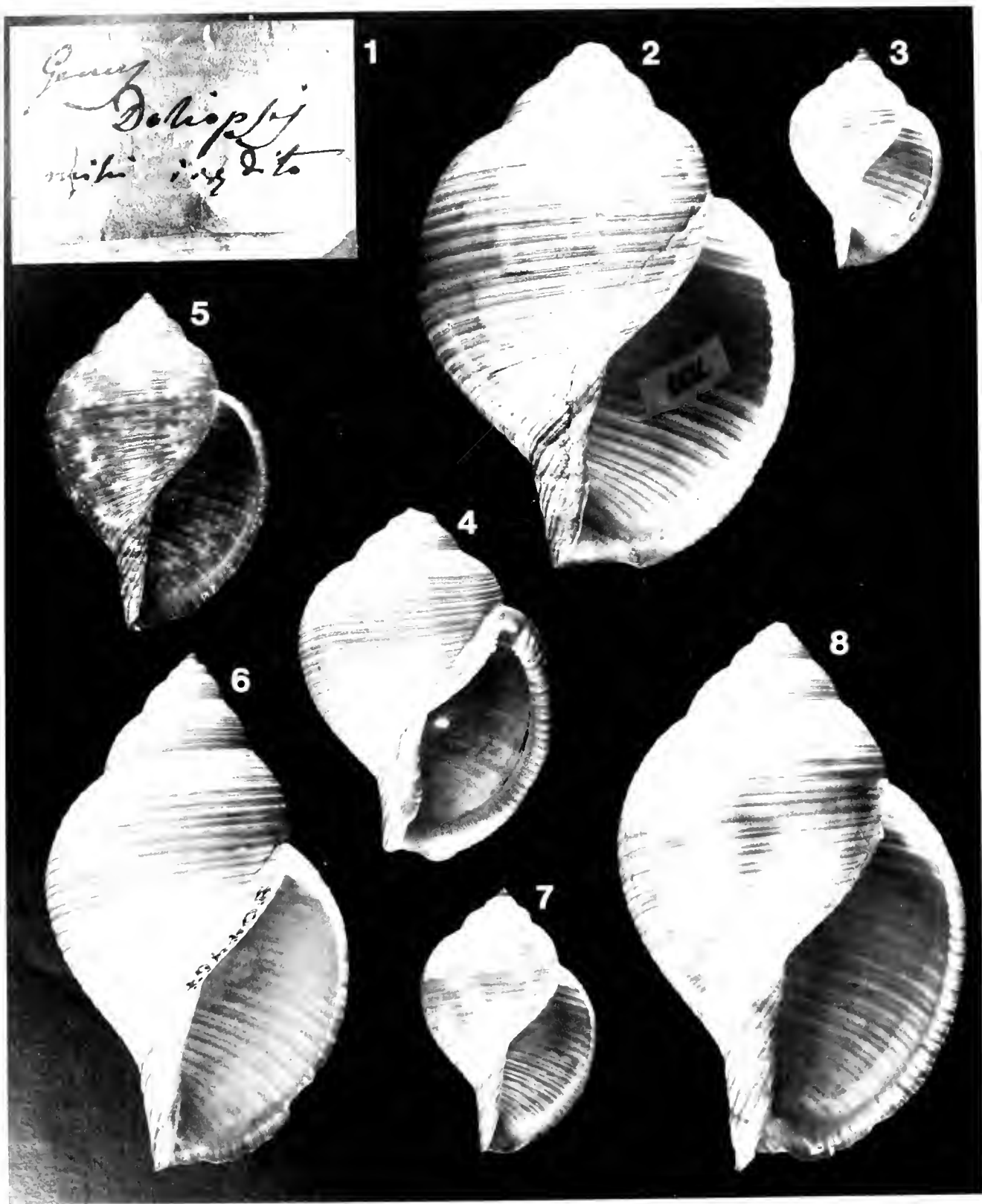
Eudolium species occur in temperate and tropical seas on soft substrata on continental shelves and slopes at 17–523 m depth. Undoubted *Eudolium* species are known from the Early Miocene [*e.g.*, *E. aoteanum* Beu, 1970 and another, unnamed species from New Zealand, *E. biornatum* Tate, 1894 from Australia] and the Oligocene [*e.g.*, *Cassidaria mutica* Michelotti, 1861]. As with *Tonna* species (Morton, 1991) the diet consists of holothurians: the gut of a specimen of *E. bairdii* from off Mayor Island, New Zealand, contained ossicles of the apodid holothurian *Protankyra rigida* Pawson, 1963 (det. D. L. Pawson). Otherwise nothing is known of *Eudolium* biology.

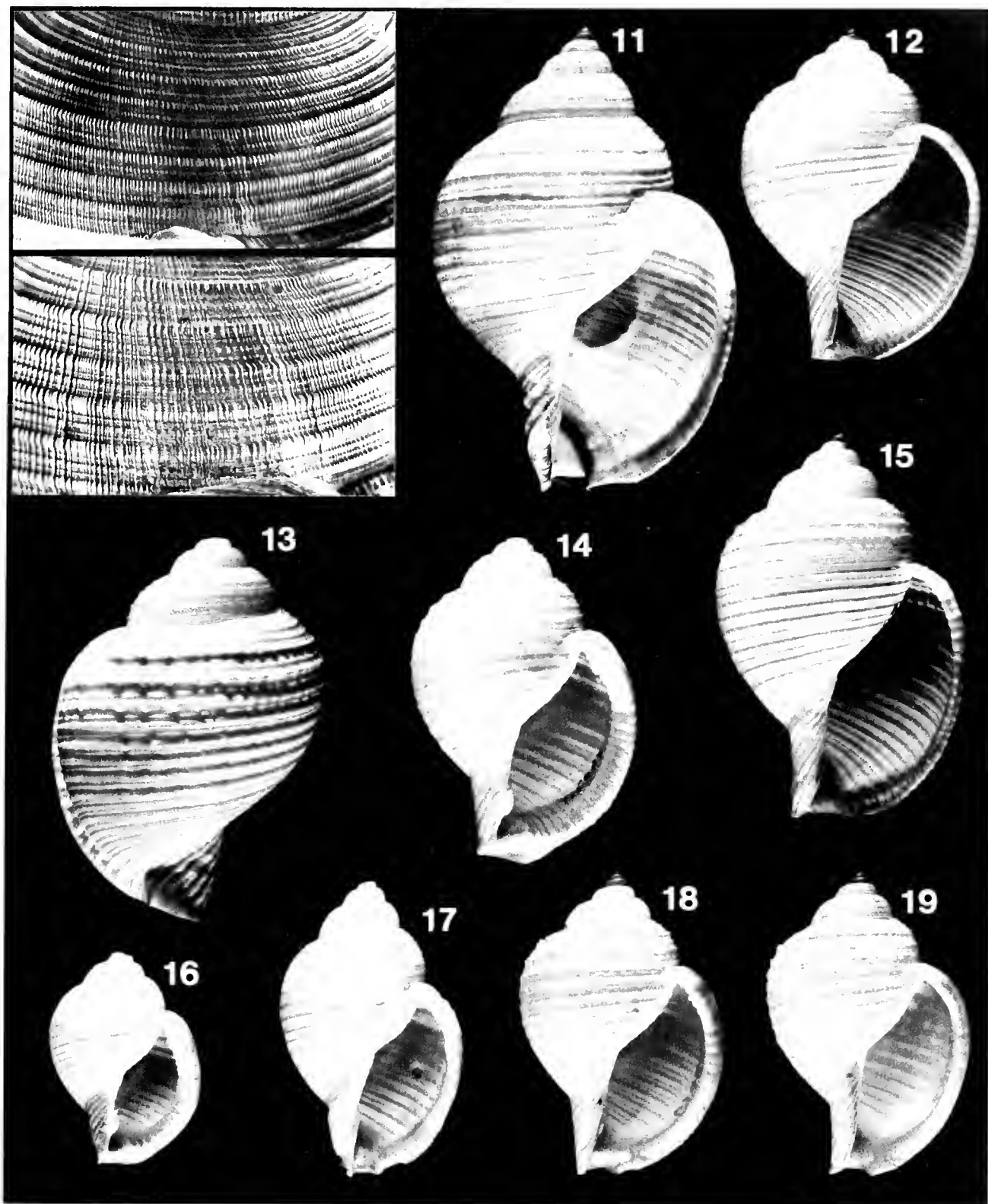
***Eudolium crosseanum* (Monterosato, 1869)**
figures 1–4, 9, 20, 23–26, 37

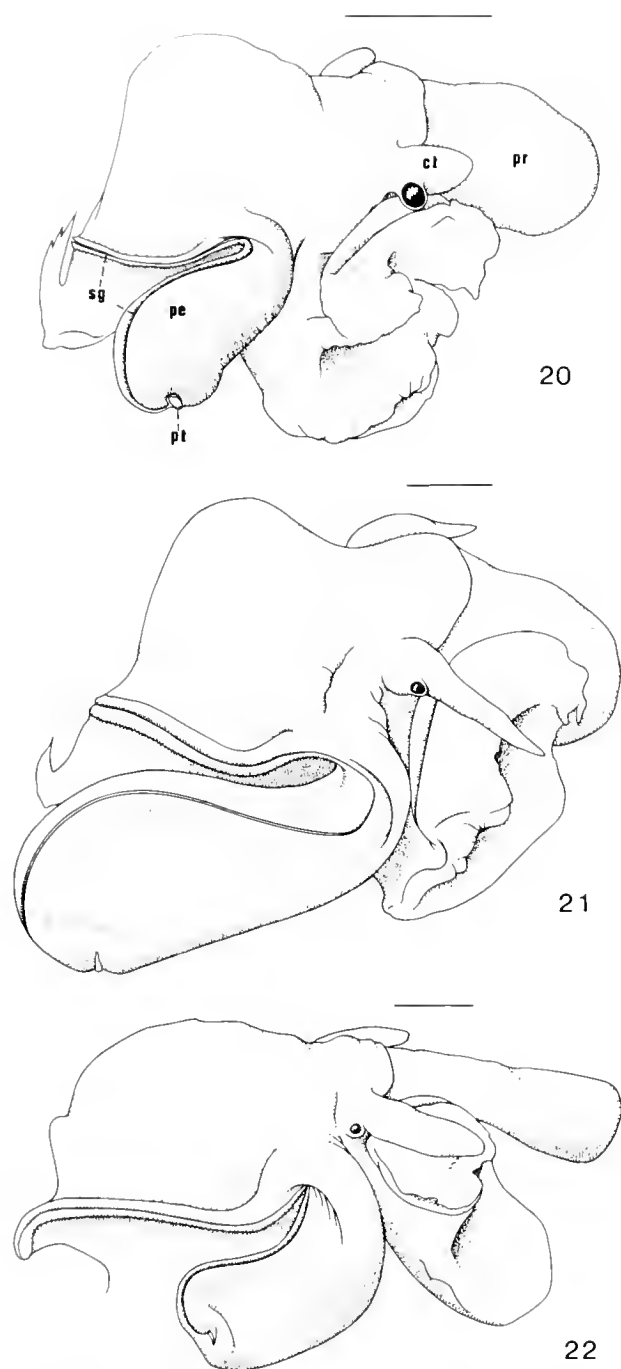
- Dolium crosseanum* Monterosato, 1869: 228, pl. 12, fig. 1. Tryon, 1855: 263, pl. 2, fig. 11 (figs 11 and 12 transposed, fig. 12 = *D. testardi* Montrouzier, 1863).
- Doliopsis crosseana* —Monterosato, 1872: 5. Coen, 1930: 147, figs 1–2 [in part—figs 6–9 = *Galeodea echinophora* Linnaeus, 1767; P. Bouchet, personal communication].
- Dolium Eudolium crosseanum* —Kobelt, 1908: 155, pl. 126, fig. 1 (in part—figs 2–3, 4 = *E. bairdii*).
- Eudolium crosseanum* —Wenz, 1941: 1076, fig. 3066. Turner, 1948: 178 (in part—pl. 81, figs 1, 2; text fig. 5 = *E. bairdii*).
- Eudolium testardi* —Osima, 1943: 132, pl. 4, fig. 3 (not *Dolium testardi* Montrouzier, 1863).
- Eudolium thompsoni* McGinty, 1955: 80, pl. 1, figs 5, 6. Abbott, 1974: 168, fig. 1788. Abbott & Dance, 1986: 119, text fig. 1 (new synonym).
- Tonna Eudolium crosseana* —Kilias, 1962: 14, fig. 12, 6. Pini, 1977: 27–38, figs 3, 6, 10 [in part—fig. 5 = *Galeodea echinophora* Linnaeus, 1767; P. Bouchet, personal communication, fig. 11 = *E. bairdii*].
- Tonna Eudolium thompsoni* —Kilias, 1962: 16, fig. 12, 5.
- NOT *Dolium Eudolium crosseanum* —Dall, 1889a,b. Dautzenberg & Fischer, 1906: = *E. bairdii*.
- NOT *Dolium crosseanum* —Locard, 1897: *Talisman* stn. 63 = *E. bairdii*, and stn. 139 = a turrid. P. Bouchet, personal communication.

Figure 1. Label in Monterosato's handwriting gummed to dorsum of holotype of *Eudolium crosseanum*. **Figures 2–4.** *Eudolium crosseanum*. 2, holotype, off Sicily, Hebrew University, Jerusalem No. 21386 (79.5 × 58 mm). 3, Oregon station 3636, off Belize, USNM 751892 (32.5 × 22 mm). 4, Oregon station 2021, off French Guiana, USNM 751885 (54 × 39.5 mm). **Figures 5–8.** *Eudolium puriforme*. 5, 7, Bohol Straits, Philippines, NMNZ MF 56381 (51 × 34.5 mm); 6, 40.5 × 27.5 mm. 7, David Starr Jordan station TC 40 54, off Oahu, Hawaii, USNM 804464 (79.5 × 47 mm). 8, Southwest of Taiwan, NMNZ MF 56380 (84.5 × 55 mm). All photographs of shells are to scale.

Figure 9. *Eudolium crosseanum* Oregon station 3636, off Belize, USNM 751892, detail of teleoconch sculpture, 7 ×. **Figures 10–19.** *Eudolium bairdii*. 10, detail of teleoconch sculpture, of specimen in figure 16, 7 ×. 11, off Aldermen Islands, New Zealand, D. Gibbs collection (76 × 49.5 mm). 12, 13, off Tosa-Shimuzu, Japan, NMNZ MF 56383 (figure 12, 51 × 37 mm, figure 13, 59 × 43.4 mm). 14, Combat station C279, Straits of Florida, USNM 715002 (49.7 × 35.5 mm). 15, off Scot Reef, Western Australia, NMNZ MF 57427 (58 × 38 mm). 16, Oregon II station 11133, off Yucatan Peninsula, Mexico, USNM 751930 (33 × 22.7 mm). 17, SMIB 4 station DW55, southwest of New Caledonia, MNHN 45 × 28.5 mm. 18, Oregon station 5690, off Colombia, USNM 751869 (46 × 31.5 mm). 19, Albatross station 5590, Sebuku Bay, Borneo, USNM 23911 (46.5 × 31.7 mm). All photographs of whole shells are to scale.







Figures 20–22. Right lateral views of head-foot areas of male *Eudolium* animals. 20. *E. crosscanum*, Oregon station 3636, off Belize, USNM 751892. 21. *E. pyriforme*, David Starr Jordan station TC/10/54, off Oahu, Hawaii, USNM 804464. 22. *E. bairdii*, Mascareignes III station 24, off Madagascar, MNHN. Scale lines. 20 = 2.5 mm; 21, 22 = 5 mm. ct, cephalic tentacle; pe, penis; pr, proboscis; pt, penial tentacle; sg, seminal groove.

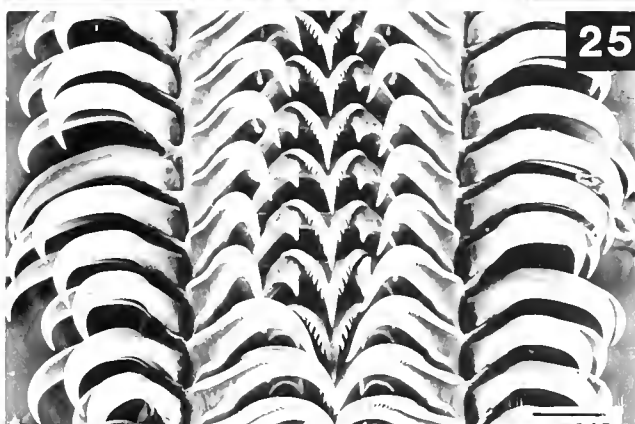
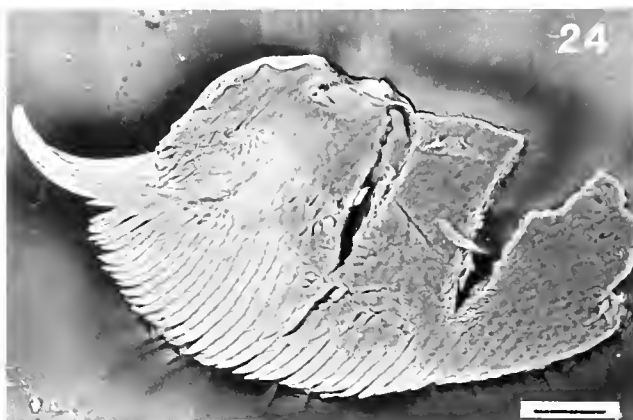
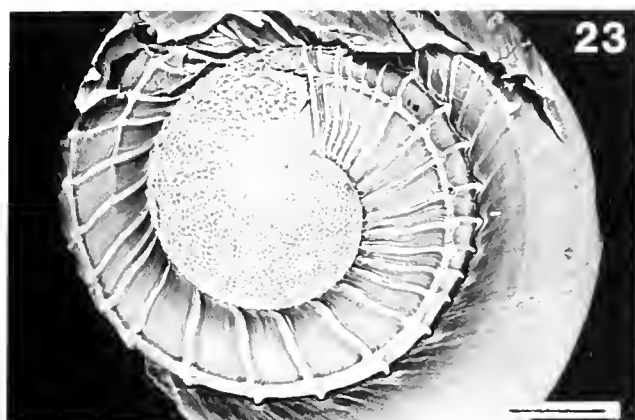
NOT *Eudolium crosscanum*.—Tomlin, 1927; Barnard, 1963; Abbott, 1974; Okutani, 1983; Kilburn, 1986; Horikoshi, 1989; Warén & Bouchet, 1990; Poppe & Goto, 1991 (= *E. bairdii*)

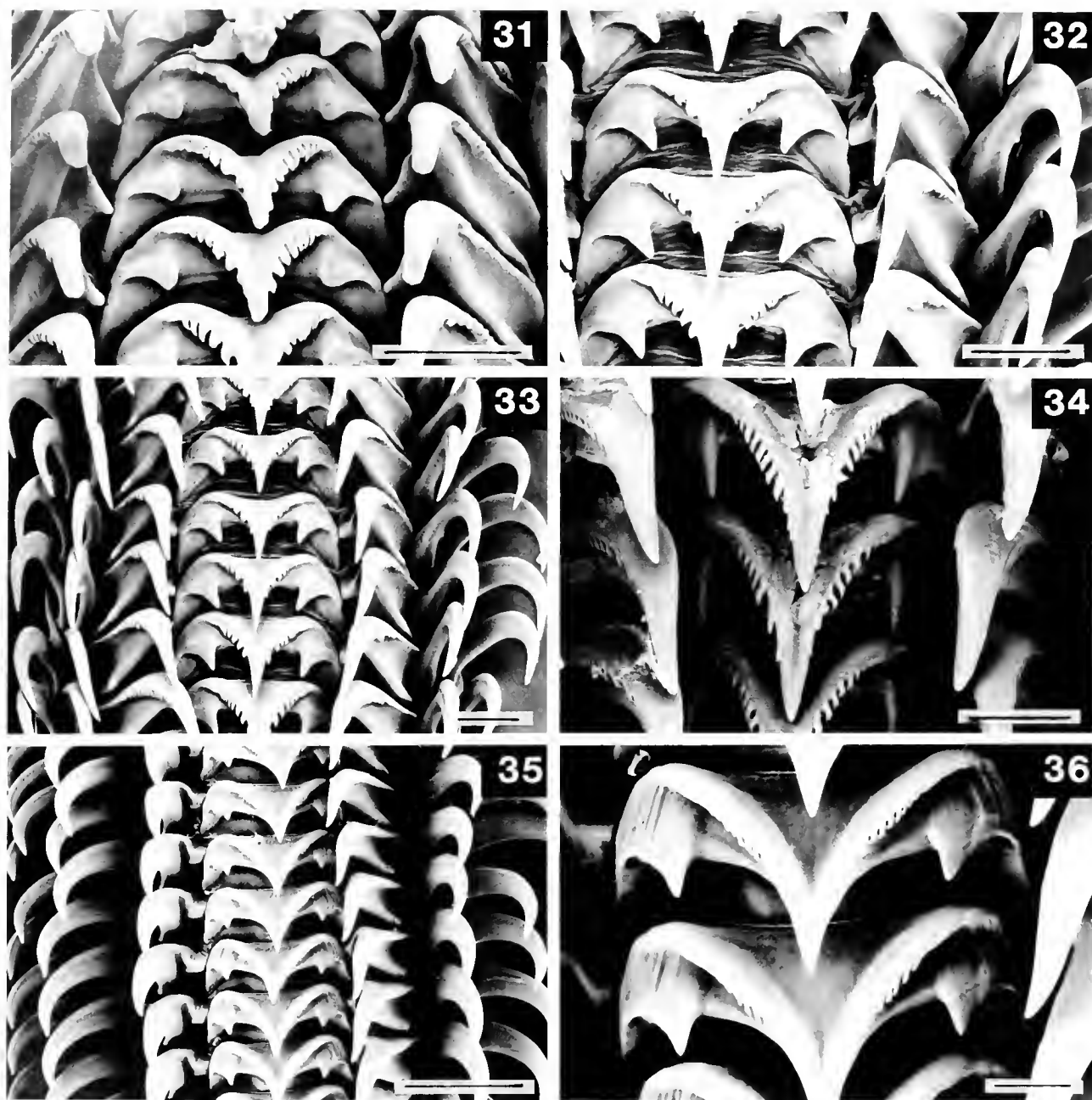
Description: Shell up to 81 mm (est.) high, thin to moderately thick, periostracum thin, straw-colored. Protoconch deep yellowish brown; teleoconch irregularly maculated with yellowish brown on a white or buff white ground, some major spiral cords with small yellowish brown spots, mature outer lip typically with a pinkish flush. Protoconch primarily conchiolin, conical, of about 5 convex whorls, 3.46–4.44 mm in diameter, sculptured with 3 rows of small periostracal spines. First whorl of calcareous mould of inner surface of protoconch (figure 23—exterior removed with sodium hypochlorite solution) 317 μ m wide, sculptured with very fine irregular network of crisp threads that enclose minute, crowded, roughly circular pits. Second whorl with fine, crisp axial riblets and 2 similar crisp spiral threads, one at shoulder angulation, the other on ramp between shoulder spiral and suture. Shoulder spiral commencing immediately, ramp spiral commencing three quarters of a whorl later. Axial ribs and spiral cords becoming obsolete early on 2nd whorl. Subsequent whorls essentially smooth, rounded. Teleoconch of up to 4 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation; and fine, crisp, crowded axial riblets; in rare specimens some spiral cords becoming very weakly nodular on last adult whorl. Thin specimens with a thin, flared, weakly dentate outer lip and smooth columella and parietal area. Thickened specimens with strongly dentate outer lip, spirally plicate columella, and with 1–3 small spirally elongate denticles on parietal area close to insertion.

Animal: (figure 20: subadult male, shell height 22.3 mm, Oregon stn. 3636) Everted proboscis large, very wide but longer than broad, thin-walled. Cephalic tentacles small, slender, rounded in cross section, gently tapered, tips rounded. Eyes small, in rounded swellings on outer sides of tentacles near bases. Penis base well behind base of right cephalic tentacle, penis very large, spatulate, laterally compressed, tip broadly rounded, deeply grooved along ventral edge to tip, minute tentacle protruding from end of groove at distal extremity. Operculum absent in adults. Jaw plates (figure 24) ovate, thin, each with strong, thickened, hooked anterior projection.

Radula: (figures 25, 26) with the formula 2.1.1.1.2, teeth curved, sharply pointed, very stout, strongly interlocked. Central tooth broad; cutting area acutely angulate, 7–9 small sharp cusps on each side, terminal cusp large, long, narrow; posterolateral projections on face strong, sharp. Lateral teeth strongly longitudinally flanged along outer

Figures 23–26. *Eudolium crosscanum*. 23. protoconch with periostracum removed, Oregon station 5914, Lesser Antilles, USNM 751903. 24. (jaw plate), 25, 26. (radula) from shell 22 mm high, Oregon station 3636, off Belize, USNM 751892. 25. width of radula. 26. detail of central, lateral and marginal teeth. Figures 27–30. *Eudolium pyriforme*. Radula from shell 41 mm high, MUSORSTOM 6 station DW391, Loyalty Islands. 27. width of radula. 28–30. details of central and lateral teeth. Scale bars: 27 = 0.5 mm, others = 0.1 mm.





Figures 31–36. *Eudolium bairdii* 31–33, radula from shell 24 mm high, Straits of Florida, Florida State Museum UF 26666. 31, detail of central and lateral teeth from anterior end of radular ribbon representing earliest teeth formed. 32, detail of central, lateral and marginal teeth at posterior third of radular—note size and morphological differences compared with teeth formed earlier (31). 33, width of radula at posterior third. 34, detail of central and lateral radular teeth from shell 57 mm high, *Mascareignes III* station 24, off Madagascar, MNHN. 35, 36, radula from shell 76 mm high, off Aldermen Islands, New Zealand, D. Gibbs collection. 35, width of radula. 36, detail of central tooth. Scale bars: 35 = 0.5 mm, others = 0.1 mm.

edges to interlock with inner marginals, terminal cusp very large, 8–11 fine cusps behind on outer edge. Marginal teeth similar, without secondary cusps.

Type data: *Dolium crosseanum*: HOLOTYPE Coen collection (No. 2521), Hebrew University, Jerusalem 21386, off Palermo, Italy; *Eudolium thompsoni*: HOLOTYPE Florida State Museum, Gainesville, Florida UF

170426, Triton stn. 1206, off Sombrero Key Light, Florida Keys, 137 m.

Other material examined: WESTERN ATLANTIC—off Cape Hatteras, South Carolina, south to off French Guiana, 35°06'N–7°18'N (56 specimens in 37 lots USNM).

Distribution: (figure 37) Mediterranean and Western Atlantic, from Cape Hatteras to French Guiana; depth

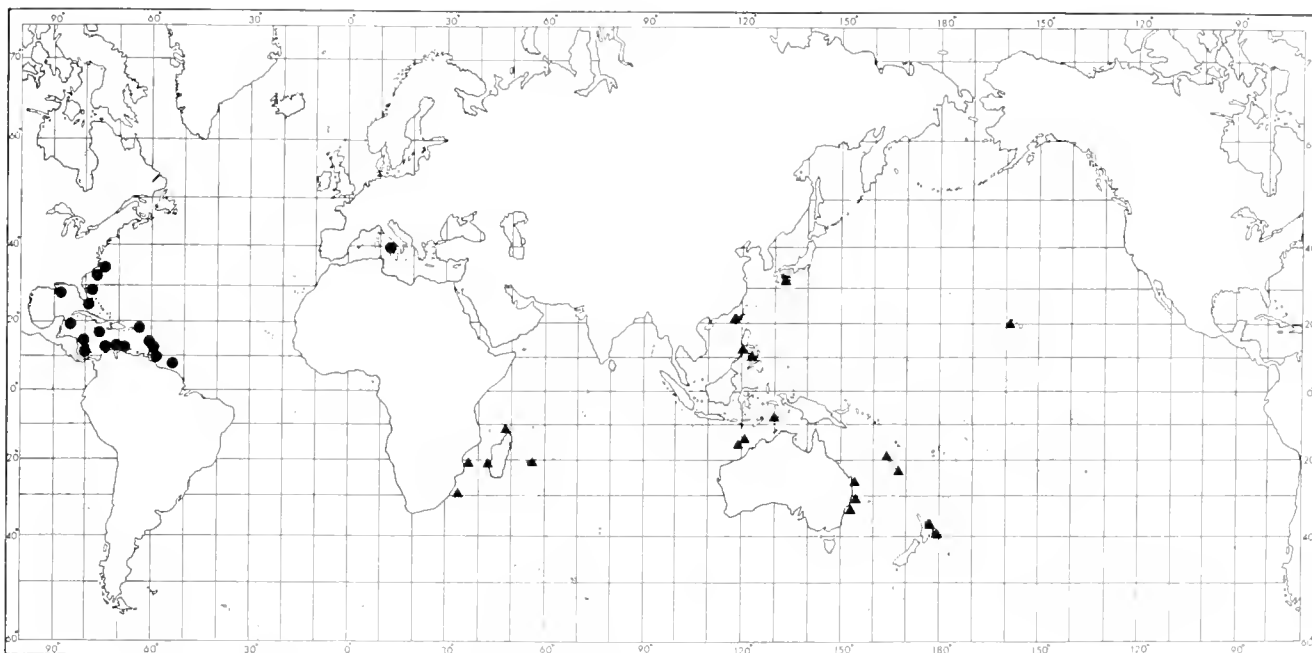


Figure 37. Map showing distribution of *Eudolium crosseanum* (●) and *E. pyriforme* (▲).

range of material examined 17–914 m, maximum known living occurrence 457 m.

Remarks: As discussed by Piani (1977) two specimens have been interpreted as the holotype of *D. crosseanum*, one in the Monterosato collection, Museo Zoologico, Roma, the other in the Coen collection, Hebrew University of Jerusalem. Piani correctly concluded that the Rome specimen cannot be the holotype because it is extensively covered by a brown periostracum and has conspicuous nodules, characters not mentioned in the rather detailed original description, and because it lacks the maculations recorded by Monterosato. From comparison of dimensions of the Rome and Jerusalem specimens with Monterosato's original published measurements, Piani (1977: 37) concluded that the Jerusalem specimen was the closest match but because there were discrepancies he suggested that it was perhaps a third example and thus by implication not the holotype. Piani (1977: figs. 6, 10) reproduced Coen's (1930: figs. 1, 2 "tipo") illustrations and a photograph (provided by H. K. Mienis) of the Jerusalem specimen. Upon receipt of the Jerusalem specimen (figures 1, 2), kindly lent to me by H. K. Mienis, it was immediately obvious that Piani's illustrations are of one and the same specimen, though this was neither unequivocally stated by Piani nor evident from the illustrations.

It transpires that the dimensions of the Jerusalem specimen were wrongly quoted by Piani (1977:37), as they in fact closely accord with Monterosato's (1869) original measurements ("long 81; diam. maj. 56 mill.; apert. 62 mill. longa, 28 lata"): height 79.8 mm (lacks protoconch—estimated height when intact 81 mm), diameter 58 mm, height of aperture 62 mm, width of aperture 28

mm. The general shell facies, color and color pattern of this specimen agree closely with the original description, while the number of denticles on the outer lip (32) are closely accordant: Monterosato stated that there were 33 denticles, but it is possible that a low swelling at the abapical extremity of the lip was also counted. The only discrepancy is the thickness of the outer lip, which ranges from 3.5 to 4.0 mm over the denticulate area, and not 3 mm as stated by Monterosato. The smooth zone at the adapical extremity, however, is 3 mm thick, suggesting that Monterosato may have measured it there to avoid including the denticles. Diagnostic features of this particular specimen that were realised on the original drawing include the distinctive pattern of chipping at the rim of the anterior siphonal canal, and the growth scar in front of the columella. Incontrovertible proof that this specimen belonged to Monterosato is the label in Monterosato's handwriting gummed to the dorsum (figure 1) "Genus Doliopsis mihi inedito".

The specific identity of the Rome specimen is uncertain, but judging from Piani's (1977: fig. 11) illustration it is much more strongly nodular than any specimen of *E. crosseanum* seen during the present study and seems more likely to be *E. bairdii* (P. Bouchet concurs). Other published records of *E. crosseanum* from the Mediterranean apart from references to the holotype are based on misidentification (see synonymy).

By direct comparison of the holotypes, the Western Atlantic *E. thompsoni* McGinty, 1955 is specifically indistinguishable from *E. crosseanum*. Judging from the fact that the species has only been obtained once in the Mediterranean yet it is relatively common in the western Atlantic, it is likely that the Mediterranean specimen is the result of a chance introduction of a teleplanic larva

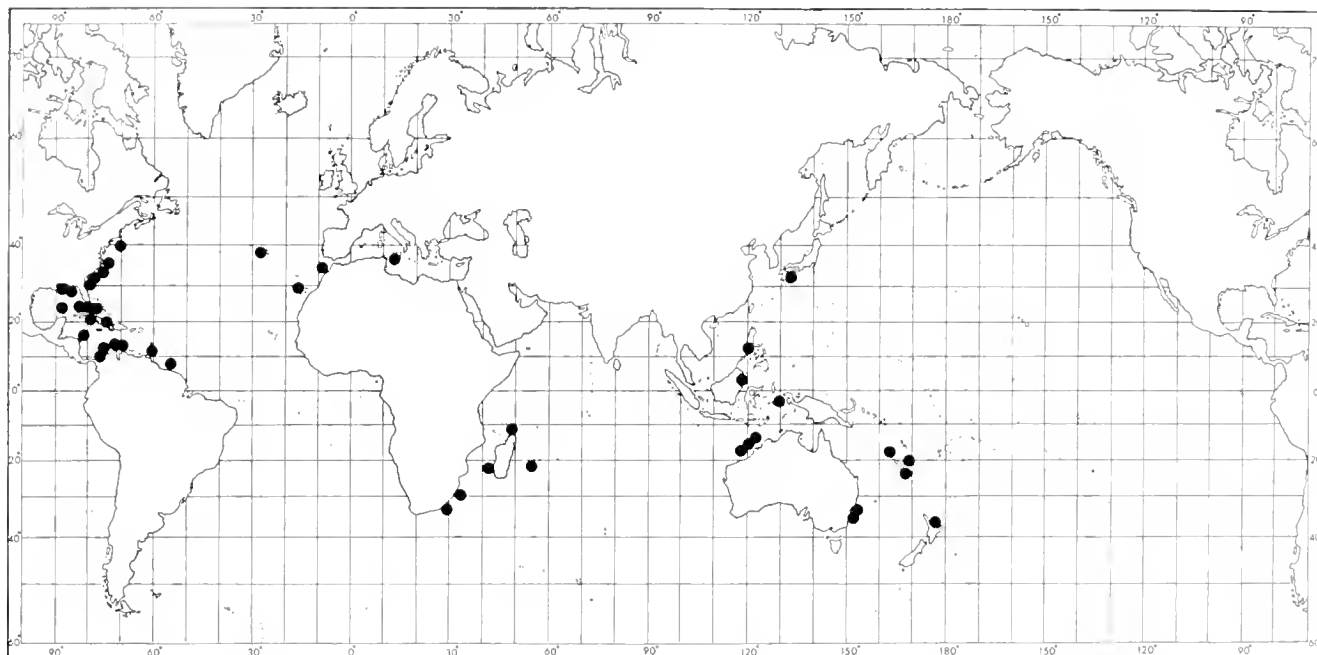


Figure 38. Map showing distribution of *Eudolium bairdii*. Eastern Atlantic distributions provided by P. Bouchet (personal communication).

transported by the Gulf Stream from Western Atlantic populations (see Discussion).

Eudolium crosseanum is closely similar to the Western Pacific and Hawaiian species *E. pyriforme* (see below).

Eudolium crosseanum was the first species described by Monterosato in an illustrious malacological career, and the holotype must have been one of his most prized possessions. He would have been impressed to know that his specimen would still be the only one known from the Mediterranean 122 years after it was described, and that it would remain the largest known example of the species.

***Eudolium pyriforme* (Sowerby, 1914)**
(figures 5–8, 21, 27–30, 37)

Dolium pyriforme Sowerby, 1914:37, pl. 2, fig. 14

Eudolium pyriforme.—Osima, 1943:131, pl. 5, fig. 4; Mayblom, 1951:282, Kira, 1959:55, pl. 22, fig. 5; Garrard, 1961:17; Kira, 1962:59, pl. 23, fig. 5; Okutani, 1964:400, pl. 1, fig. 23, text fig. 2; Habe & Kosuge, 1967:66, pl. 25, fig. 12; Kuroda, Habe & Oyama, 1971:135, pl. 37, fig. 4; Wolfe, 1974:3, text fig.; Powell, 1974:201; Cernohorsky, 1976:1, fig. 1; Cernohorsky, 1978:61, pl. 16, fig. 7; Powell, 1979:163; Kosuge, 1985:59, pl. 22, fig. 6; Abbott & Dance, 1986:116, text fig.; Kilburn, 1986:4, fig. 11; Okutani, 1988:78, fig. 46

Description: *Shell* up to 85.5 (est.) mm high, thin; periostracum thin, translucent, straw-colored. Protoconch yellowish brown; teleoconch sparsely to densely irregularly maculated with pale to deep yellowish brown, major spiral cords alternately spotted yellowish brown and white on a buff white ground, outer lip of many specimens

with a pinkish flush. Protoconch primarily conchiolin, of about 5 convex whorls, 2.95–3.45 mm in diameter, essentially smooth (worn?). Internal calcareous mould not seen. Teleoconch of up to 4.6 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation, and fine axial riblets, axials crisp on first 3 whorls, less crisply defined on subsequent whorls, no nodules. Outer lip of most specimens weakly thickened in adults, but a few specimens are moderately thickened and dentate; columella and parietal area simple.

Animal: (figure 21—adult male minus radula that had been extracted when received from one of 7 shells 64–79.5 mm in height, from off Oahu, Hawaii—USNM 804464) externally similar to that of *E. crosseanum* (see above) but differing in that the penis arises nearer outer base of right cephalic tentacle. Jaw similar to that in *E. crosseanum*.

Radula: (figures 27–30—juvenile female 22 mm shell height, *Orcgon* stn. 3636, off Belize City, USNM 751892) similar to that of *E. crosseanum* except that central and lateral teeth have smaller cusps, and sides of central tooth subparallel instead of markedly tapered.

Type data: *Dolium pyriforme*: HOLOTYPE: The Natural History Museum, London 1915.1.6.148, off Kii, Japan.

Other material examined (73 specimens): INDIAN OCEAN—Trawled off Umgababa, Natal, South Africa (1 NMP); trawled off Durban, South Africa, 421 m (1 NMP); trawled off Bazaruto I., Mozambique (1 NMP); 12°39.8'S, 48°16.2'E, N Madagascar, 375–385 m (1 MNHN); 12°42.4'S, 48°14.3'E, N Madagascar, 285–295

m (1 MNHN); 12°42.9'S, 48°12.1'E, N Madagascar, 445–455 m (1 MNHN); 12°43'S, 48°15'E, 300–340 m (1 MNHN); 20°58'S, 55°15'E, off Réunion, 450–580 m (1 MNHN); 22°14.7'S, 43°04.5'E, S Madagascar, 470–475 m (1 MNHN); *Crevettiere* 1986 stn. 80, 22°17'S, 43°04'E, SW Madagascar, 530 m (1 MNHN); *Crevettiere* 1986 stn. 76, 22°22'S, 43°03'E, SW Madagascar, 530 m (2 MNHN); *Crevettiere* 1986 stn. 56, 22°26'S, 43°05'E, SW Madagascar, 435 m (2 MNHN); *Crevettiere* 1986 stn. 57, 22°26'S, 43°06'E, SW Madagascar, 460 m (1 MNHN); *Crevettiere* 1986 stn. 58, 22°26'S, 43°06'E, SW Madagascar, 440 m (1 MNHN); *Socla* stn. 01/84/74, 14°16.5'S, 122°54.4'E, NW of Collier Bay, Western Australia, 302 m (1 WAM); *Socla* stn. 01/84/54, 15°51.2'S, 120°44.3'E, WNW of Lacepede Archipelago, Western Australia, 350–348 m (6 WAM) JAPAN—off Tosa Shimuzu, *ca.* 350–400 m (1 NMNZ); off Ashizuri-misaki (2 MCZ); off Tosa, *ca.* 183 m (1 MCZ); off Kii (1 MCZ). TAIWAN—SW of Taiwan, *ca.* 128–183 m (5 NMNZ). PHILIPPINES—*Albatross* stn. 5289, Batangas Bay, Luzon, 315 m (2 USNM); *Coriolis* MUSORSTOM 3 stn. CP103, of Mindoro, 193–200 m (1 MNHN); *Coriolis* MUSORSTOM 2 stn. CP83, 13°55'N, 120°30'E, off Mindoro, 318–320 m (1 MNHN); Bohol Straits, *ca.* 200 m (5 NMNZ); *Albatross* stn. 5519, off Pt Tagalo, N. Mindanao, 333 m (2 USNM); *Albatross* stn. 5518, off Pt Tagalo, Mindanao, 366 m (2 USNM); 9°43'S, 130°00'E, Timor Sea, *ca.* 250 m (2 NMNZ). HAWAII—*David Starr Jordan* stn. TC-40-54, 21°01.6'N, 156°43.00'W, off Oahu, 223 m (7 USNM). QUEENSLAND and NEW SOUTH WALES—Off Cape Moreton, 165 m (1 AMS); *Kapala* stn. 71-08, *ca.* 32°46'S, 152°16'E, off Newcastle, 280–549 m (1 AMS); *Kapala* stn. K75-05-03, 33°02'S, 152°31'E, off Newcastle, 475 m (1 AMS); between Newcastle and Sydney, 182–549 m (1 AMS); off Broken Bay, 137 m (1 AMS); between Sydney and Norah Head, 412–457 m (1 AMS); *Kapala* stn. K76-07-01, 33°33'S, 151°59'E, off Broken Bay, 384 m (1 AMS); *Kapala* stn. K76-24-05, 33°33'S, 151°59'E, off Broken Bay, 373–366 m (1 AMS); off Sydney, 420–440 m (1 AMS); 35°50'S, 150°34'E, off Batemans Bay, 366 m (1 AMS). CHESTERFIELD REEFS—*Coriolis* MUSORSTOM 5 stn. 376, 19°51'S, 158°30'E, 280 m (1 MNHN). NEW CALEDONIA—*Vauban* MUSORSTOM 4 stn. CP193, 18°56'S, 163°23'E, off d'Entrecasteau Reefs, 415 m (1 MNHN); *Vauban* SMIB 3 stn. DW28, 22°47'S, 167°12'E, 394 m (1 MNHN); *Vauban* SMIB 1 stn. DW2, 22°52'S, 167°13'E, 415 m (1 MNHN); *Vauban* SMIB 2 stn. DW15, 22°53'S, 167°11'E, 375–402 m (1 MNHN); *Vauban* SMIB 2 stn. DW8, 22°54'S, 167°13'E, 435–447 m (1 MNHN); *Vauban* SMIB 2 stn. DW17, 22°55'S, 167°15'E, 428–448 m (1 MNHN). LOYALTY ISLANDS—*Alis* MUSORSTOM 6 stn. DW391, 20°47'S, 167°06'E, off Ouvéa, 390 m (1 MNHN); *Alis* MUSORSTOM 6 stn. CP 465, 21°04'S, 167°32'E, off Lifou, 480 m (1 MNHN). NEW ZEALAND—off Aldermen I., *ca.* 366 m (1 Gardner coll'n, Auckland); B8843 (0.589), 37°14.6'S, 176°51.0'E, Rangatira Knoll, NW of White I., 407–162 m (fragment NMNZ); off Tokomaru Reef, Gisborne, *ca.* 220 m (1 Auckland Institute and Museum).

Distribution (figure 37): Southern Africa, Madagascar, Réunion, Japan, Taiwan, Philippine Islands, Indonesia, Hawaii, Australia, New Caledonia, northern New Zealand; depth range of material examined 137–580 m, deepest known living occurrence 390 m.

Remarks: *Eudolium pyriforme* is extremely similar to *E. crosseanum* in shell color, color pattern, protoconch morphology, shell thickness, size relative to the number of whorls, and in size attained. Although they are also similar in sculpture, *E. pyriforme* differs in having axial riblets that are consistently lower, broader and less sharply defined than those of *E. crosseanum*, especially where traversing the spiral cords. As described above, a single adult male specimen of *E. pyriforme* differs from that of an immature *E. crosseanum* in having the penis base close beside the right cephalic tentacle instead of well behind it (figures 20, 21). The external anatomies of males and females are otherwise similar. Although the position of the penis seems likely to be a major distinguishing feature, with only two different-sized animals for comparison it is impossible to ascertain whether or not its position is infraspecifically stable or changes during ontogeny.

As described and illustrated herein (figures 25–30), the radula of *E. pyriforme* differs from that of *E. crosseanum* in the shape of the central tooth and in the size of the secondary cusps. With only a single radula from each species from dissimilar-sized specimens, however, it is impossible to ascertain either the degree of infraspecific variability at equivalent size, or the degree of morphological change during ontogenetic development (see *E. bairdii* below).

Specimens of *E. pyriforme* tend to be a little narrower than those of *E. crosseanum*, although there is a broad overlap in shape. Shell height/diameter ratio in *E. pyriforme* ranges from 1.41 to 1.72 (mean 1.53, SD 0.095, $n = 30$) as against 1.31–1.66 (mean 1.44, SD 0.085, $n = 18$) in *E. crosseanum*. Specimens from off Hawaii are uniformly narrowly ovate (USNM 804464, height/diameter ratio 1.59–1.72, mean 1.67, SD 0.047, $n = 7$, figure 6). Some specimens from Japan (MCZ 293903), the Timor Sea (NMNZ MF.57428), New South Wales (AMS C.68870) and Mozambique (NMP H.7800) are as narrowly ovate as specimens from Hawaii, however, and there is complete integration between narrow and broad forms in material from west of Hawaii (height/diameter ratio 1.41–1.62, mean 1.48, SD 0.052, $n = 22$).

Eudolium bairdii (Verrill & Smith, 1881)
(figures 10–19, 22, 31–36, 38)

Dolium bairdii Verrill & Smith in Verrill, 1881:299; Verrill, 1882:515, Verrill, 1884:253, pl. 29, figs. 2a,b

Dolium bayardi (sic.).—Paetel, 1888:221

Dolium (*Eudolium*) *crosseanum*.—Dall, 1889a:232 (in part), pl. 15, fig. 5

Dolium (*Eudolium*) *crosseanum*.—Dall, 1889b:134, pl. 15, fig. 5, pl. 44, fig. 2, pl. 62, figs. 83, 83a; Dautzenberg & Fischer, 1906:38 (not *D. crosseanum* Monterosato, 1869).

- Dolium crosseanum*.—Locard, 1897:293 (in part not *D. crosseanum* Monterosato, 1869—*Talisman* stn. 139 record is based on a turrid; P. Bouchet, personal communication).
- Dolium* (*Eudolium*) *crosseanum* var. *solidior* Dautzenberg & Fischer, 1906:38, pl. 3, fig. 1 (*new synonym*).
- Dolium* (*Eudolium*) *crosseanum*.—Kobelt, 1908:155, pl. 126, figs. 2, 3, 4 (in part—fig. 1 = *E. crosseanum*).
- Morio lineata* Schepman, 1909:124, pl. 10, fig. 5 (*new synonym*).
- Eudolium crosseanum*.—Tomlin, 1927:82, fig. 4b; Barnard, 1963:8, Abbott, 1974:165, pl. 6, fig. 1787; Okutani, 1983:264, text fig.; Kilburn, 1986:4, fig. 12; Horikoshi, 1989:63, pl. 15, fig. 11; Warén & Bouchet, 1990:89, figs. 11, 78, 79; Poppe & Goto, 1991:128, pl. 22, figs. 1, 2 (not *D. crosseanum* Monterosato, 1869).
- Eudolium lineatum*.—Osima, 1943:133, pl. 5, fig. 1.
- Oocorys lineata*.—Turner, 1948:178, 190, Abbott & Dance, 1986:116, text fig.
- Eudolium inflatum* Kuroda & Habe, 1952:56 (replacement name for *Eudolium lineatum* Osima not Schepman); Kuroda & Habe, 1957:28, figs. 2, 4, 5; Kira, 1962:59, pl. 23, fig. 4; Okutani, 1988:77, fig. 45; Bieler & Petit, 1990:137 (*new synonym*).
- Eudolium lineatum inflatum*.—Kira, 1954:44, pl. 22, fig. 4, Kira, 1959:55, pl. 22.
- Eudolium kuroharai* Azuma, 1960:98, pl. 1, fig. 8, text fig. 1 (*new synonym*).
- Tonna* (*Eudolium*) *crosseana*.—Kiliyas, 1962:14 (in part).
- Dolium* (*Eudolium*) *crosseanum solida* (sic).—Settepassi, 1971, appendix vii, text figs.
- Tonna* (*Eudolium*) *crosseana*.—Piani, 1977, fig. 11.
- Oocorys solidior*.—Piani, 1977:38, figs. 1, 2, 7.

Description: *Shell* up to 75.5 mm high, thin to rather thick, periostracum thin, straw-colored. Protoconch deep yellowish to reddish brown; teleoconch white or buff white, major spiral cords yellowish to reddish brown, outer lip white. Protoconch primarily conchiolin, conical, of about 5 convex whorls, 3.00–4.75 mm in diameter, sculptured with 3 narrow spiral threads with small spines (in well preserved specimens). Calcareous mould of inner surface of protoconch (Warén & Bouchet, 1990: fig. 79) similar to that of *E. crosseanum* but with 3 instead of 2 spiral threads. Teleoconch of up to 4.4 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation, and fine axial riblets, axials less crisply defined after third whorl, last adult whorl with or without weak to strong nodules on major spiral cords. Shell ranging through intermediates from thin to rather thick. Thin specimens with thin, flared, weakly dentate outer lip and simple columella and parietal area. Most thickened specimens with thick, strongly dentate outer lip, thick spirally plicate callus at base of columella, and 1–3 spirally elongate denticles on parietal area below insertion.

Animal: (figure 22, adult male, shell height 57.5 mm, *Mascareignes III* stn. 24, off Madagascar) externally similar to that of *E. pyriforme*.

Radula: (figures 31–36) (from shells 25, 57 and 76 mm in height) similar to those of *E. crosseanum* and *E. pyriforme*. With increasing size central and lateral teeth

enlarging while size of secondary cusps and area they occupy remain rather static. Secondary cusps ultimately becoming obsolete on laterals in large adults.

Type data: *Dolium bairdii*: HOLOTYPE USNM 51385 (51 × 25 mm), *Fish Hawk* station 945, 39°58'N, 71°13'W, off Barnegat, New Jersey, 379 m; *Dolium* (*Eudolium*) *crosseanum* var. *solidior*: HOLOTYPE Musée Océanographique, Monaco, 38°52.50'N, 27°23.05'W, off the Azores, 599 m; *Morio lineata*: HOLOTYPE Zoological Museum, Amsterdam 3.09.008, *Siboga* stn. 173, 3°27'S, 131°0.5'E, Ceram Sea, 567 m; *Eudolium inflatum*: TYPE MATERIAL (Osima, 1943, pl. 5, fig. 1) possibly in Oshima collection, which was destroyed during World War II (A. Matsukuma, personal communication), off Wakayama Prefecture, Japan; *Eudolium kuroharai*: HOLOTYPE in Mr. M. Azuma's private collection, Takarazuka City, Japan (not seen), off Tosa, Japan.

Other material examined (161 specimens): WESTERN ATLANTIC OCEAN—Barnegat, New Jersey, south to off French Guiana, 39°58'N–7°37'N (12 specimens in 9 lots MCZ, 91 specimens in 43 lots USNM). WESTERN INDIAN OCEAN—12°01'S, 49°26'E, off Madagascar, 450 m, A. Crosnier (1 MNHN); 12°42'S, 48°14'E, off N. Madagascar, 380–375 m, A. Crosnier (1 MNHN); 12°43'S, 48°12'E, off N. Madagascar, 445–455 m, A. Crosnier (1 MNHN); *Marion-Dufresne* cruise 32, stn. CP 144, 20°50'S, 55°35'E, off Réunion, 605–620 m (1 MNHN); *Mascareignes III* stn. 37, 22°18'S, 43°05'E, off S Madagascar (1 MNHN); *Crevettiere* 1986 stn. 80, 22°17'S, 43°04'E, SW Madagascar, 530 m (1 MNHN); *Crevettiere* 1986 stn. 81, 22°23'S, 43°03'E, SW Madagascar, 525 m (2 MNHN); *Mascareignes III* stn. 24, 22°31'S, 43°07'E, off S Madagascar, 430–460 m (1 MNHN); trawled off Umgababa, Natal, South Africa (1 NMP); trawled off Tongaat, Natal, South Africa (1 NMP); off Cape St. Francis, South Africa (1 NMP). WESTERN AUSTRALIA—off Augustus I. south to off Rowley Shoals (2 specimens in 1 lot NMNZ, 23 specimens in 19 lots WAM, 1 specimen USNM). JAPAN—SW of Ashizuri misaki, Kochi Prefecture, trawled (1 MCZ); off Tosa Shimuzu, Kochi Prefecture, 350–400 m (2 NMNZ). PHILIPPINES—*Coriolis* MUSORSTOM 3 stn. CP106, 13°47'N, 120°30'E off Mindoro, 640–668 m (1 MNHN). MALAYSIA—*Albatross* stn. 5592, Sebuku Bay, Borneo, 558 m (1 USNM); *Albatross* stn. 5590, Sebuku Bay, Borneo, 567 m (1 USNM). NEW CALEDONIA—*Vauban* MUSORSTOM 4 stn. DW156, 18°54'S, 163°19'E, Grand Passage, 525 m (1 MNHN); *Vauban* MUSORSTOM 4 stn. DW197, 18°51'S, 163°21'E, Grand Passage, 550 m (1 MNHN); *Vauban* MUSORSTOM 4 stn. CP 171, 18°58'S, 163°14'E, Grand Passage, 425 m (1 MNHN); *Jean-Charcot* BIOCAL stn. DW36, 23°09'S, 167°11'E, 650–680 m (1 MNHN); *Alis* SMIB 4 stn. DW55, 23°21'S, 168°05'E, 215–260 m (1 MNHN). LOYALTY ISLANDS—*Alis* MUSORSTOM 6 stn. CP 467, 21°05'S, 167°32'E, off Lifou, 575 m (1 MNHN). NEW SOUTH WALES—off Port Stephens south to off Brush I. (5 specimens in 5 lots AMS). NEW ZEALAND—N of Mayor I., Bay of Plenty, 380–420 m,

coll. M. Huaki (1 NMNZ); off Aldermen L., New Zealand, 400 m (1 D. Gibbs coll'n, Auckland).

Distribution (figure 38): Atlantic, Mediterranean and Indo-Western Pacific, 17–823 m, deepest known occurrence of living specimen 560 m.

Remarks: *Eudolium bairdii* is rendered highly distinctive by the reddish to yellowish brown spiral bands on the major spiral cords, a pattern in marked contrast to the irregular mottling of *E. crosseanum* and *E. pyriforme*. *Eudolium bairdii* is indistinguishable from the Pacific form that has usually been known as *E. lineatum* (see below). Compared with *E. crosseanum* and *E. pyriforme* at the same stage of growth, the primary spiral cords in *E. bairdii* tend to be more prominent, while the secondary spirals generally enlarge more slowly relative to the primaries. *E. bairdii* differs further in having considerably stronger axial riblets, especially where traversing the spiral cords. The axial riblets in *E. bairdii* tend also to be less crowded, numbering 3–7 per millimeter at the end of the second teleoconch whorl (mean 5.40, SD 1.04, $n = 20$), compared with 6–10 (mean 8.33, SD 1.07, $n = 12$) in *E. crosseanum*, and 6–11 (mean 8.69, SD 1.55, $n = 13$) in *E. pyriforme*. The calcareous internal mould of the protoconch of *E. bairdii* (Warén & Bouchet, 1990: fig. 79—misidentified as *E. crosseanum*) differs from that of *E. crosseanum* (figure 23) in having 3 instead of 2 spiral threads. With only a single protoconch from each species for comparison, however, the degree of infraspecific variability in protoconch morphology is uncertain.

Of the three known living *Eudolium* species, *E. bairdii* exhibits the greatest variation in shell morphology, undoubted adults ranging from 32.5 mm (est.) to 75.5 mm in height, with lightly built or strongly thickened shells, and with or without nodules on the last adult whorl. There is smooth intergradation between all of the extremes both within and between samples from the Atlantic and the Indo-Pacific. By direct comparison of holotypes and topotypes, I am unable to detect any constant differences between *D. bairdii*, *D. crosseanum* var. *solidior*, *M. lineatum*, *E. inflatum* and *E. kuroharai*, and so it is concluded that they are all conspecific. It is significant, however, that thick-shelled forms with heavily thickened outer lips and strongly dentate apertures (extreme *solidior* form) (figures 14, 16) have no strict parallel (figure 17) outside the Atlantic, while specimens from off eastern Australia are thick-shelled and often particularly heavily sculptured, yet they do not exhibit the apertural features of the *solidior* form. These differences suggest that there may have been some genetic drift between isolated, probably largely self-recruiting populations, but these may also be non-genetic responses to local environmental conditions. The latter interpretation is suggested by the fact that a *solidior*-like form is also rarely exhibited by the Atlantic *E. crosseanum* (figure 4) yet not by *E. pyriforme*, its Indo-Pacific sister species. Heavy shelled forms (estimated height 34.5–61.0 mm) are clearly adults and perhaps senescent, and it is

likely that many lightly built forms (32.5–75.5 mm) are also mature. Although type specimens of *D. bairdii* and the synonymized taxa are not illustrated here, illustrations of strongly similar specimens are provided for orientation: *D. bairdii*, *E. inflatum* and *E. kuroharai* (figures 12, 13, 15), *D. crosseanum* var. *solidior* (figures 14, 16), *Morio lineata* (figures 18, 19).

E. bairdii and *E. crosseanum* have fully overlapping geographic and bathymetric ranges in the Atlantic (figures 37, 38), and the two species have been taken together at three stations in the Western Atlantic (*Oregon* stn. 2391, USNM 878126 and 751929 respectively; *Oregon* stn. 4911, USNM 878128 and 751872; *Oregon II* stn. 11253, USNM 766104 and 878129). *E. bairdii* and *E. pyriforme* also have overlapping, geographic and bathymetric ranges and are thus probably locally sympatric.

DISCUSSION

Although larvae of *Eudolium* species have not been observed in the field or reared in the laboratory, the protoconch morphology and species distributions are characteristic of tonnoideans with teleplanic larvae (Scheltema, 1966; Laursen, 1981). Teleplanic larvae remain planktonic for many months, in some species for a year or more, and can be transported great distances in ocean currents (Scheltema, 1966, 1971; Pechenik *et al.*, 1984). Species with teleplanic larvae often have extremely wide amphioceanic, Indo-Pacific, or Indo-Pacific-Atlantic distributions in their benthic stage, especially those with wide tolerances (Scheltema, 1986 and references therein). Although some localities for individuals in the benthic stage do not necessarily support self-recruiting populations, it is clear that widely separated self-recruiting populations are able to maintain their specific integrity through periodic influx of larvae from up-current populations.

Whether or not Eastern Atlantic and Mediterranean specimens respectively of *E. bairdii* and *E. crosseanum* arose from local self-recruiting populations is unknown, but judging from the fact that they are indistinguishable from Western Atlantic specimens and that both species are evidently far more common in the Western Atlantic than in the Mediterranean, it is probable that some if not all originated from Western Atlantic larvae that were transported by the Gulf Stream (Scheltema, 1986). While *E. bairdii* may well be at least partly self-recruiting in the Eastern Atlantic, this is unlikely to be true for *E. crosseanum* in the Mediterranean with a single confirmed specimen. Specific integrity of the strongly isolated Hawaiian population of *E. pyriforme* is probably maintained through intermittent recruitment of larvae from the Western Pacific via the Kuroshio Current (Zinsmeister & Emerson, 1979).

It is likely that the two most closely related species, *E. crosseanum* and *E. pyriforme* originated from disjunct populations of an ancestor that formerly had a continuous distribution in the Tethyan Atlantic-Indo-Pacific. Since *Eudolium* species are unknown living ei-

ther in the Eastern Pacific or from the Western Atlantic south of Columbia, it seems probable that distribution was continuous via Africa rather than America. Unfortunately, the southwestern coast of Africa has been relatively poorly sampled at depths most likely to yield *Eudolium* species (300–600 m) and it is unknown whether or not they occur there. The apparent absence of *E. crosseanum* off South Africa suggests that larvae are incapable of reaching there from northeastern South America in the great counterclockwise South Atlantic gyral. Similarly, larvae of *E. pyriforme* in the warm Agulhas Current are perhaps unable to survive injection into the Atlantic Ocean via the cold Benguela Current. Atlantic and Indian Ocean populations of *E. bairdii* may be fully isolated by the same means. Unless hydrological conditions off southwest Africa were formerly more favorable, perhaps during Pleistocene interglacials, *E. bairdii* and the ancestor of *E. crosseanum* and *E. pyriforme* may have ranged through the circumtropical Tethys Ocean, in which case isolation of eastern and western populations would date from the late Miocene following establishment of the Middle Eastern Landbridge (Por, 1986 and references therein). The second alternative is favored here.

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Buridrillia deroyorum, New Species from the Galapagos Islands, a Living Record of a Neogene Turrid Genus

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ABSTRACT

Buridrillia deroyorum new species is described from 310 meters off Isla Floreana (type locality) and 365 meters off Isla Duncan, Galapagos Islands. It is the first living species of a turrid genus otherwise known from Neogene fossils from the New World tropics. The genus is assigned to Crassispirinae on shell and radular characters. It has a columellar plication, evidently convergent with that of Borsoniinae.

Key Words: Prosobranch gastropod; Turridae; Crassispirinae; *Buridrillia* new species; Galapagos Islands, Ecuador

INTRODUCTION

André and Jacqueline DeRoy were for many years avid collectors of Galapagan marine mollusks and are knowledgeable students of the molluscan fauna of the archipelago. Mr. DeRoy was a commercial fisherman who undertook numerous dredging operations, and Mrs. DeRoy spent much of her time collecting in shallow waters. For the past 30 years, they have contributed specimens to the American Museum of Natural History and the Natural History Museum of Los Angeles County for study and report. Among these specimens is a new species of turrid gastropod collected in the 1970s. We take great pleasure in describing this new turrid in honor of the DeRoys.

The species described here is of more than usual interest for two reasons: it represents the first living record of a genus previously believed to have become extinct in the late Neogene, and study of its radular characters results in its assignment to a subfamily other than that which comes to mind upon first examination of shell morphology.

Abbreviations for institutions used in the text: AMNH—American Museum of Natural History, New York; LACM—Los Angeles County Museum of Natural History, Los Angeles.

SYSTEMATICS

Family TURRIDAE Swainson, 1840

Subfamily CRASSISPIRINAE Morrison, 1966

Genus *Buridrillia* Olsson, 1942

Type species (original designation): *Clathrodrillia* (*Buridrillia*) *panarica* Olsson, 1942:51. Pliocene of the Burica Peninsula, Panama and Costa Rica.

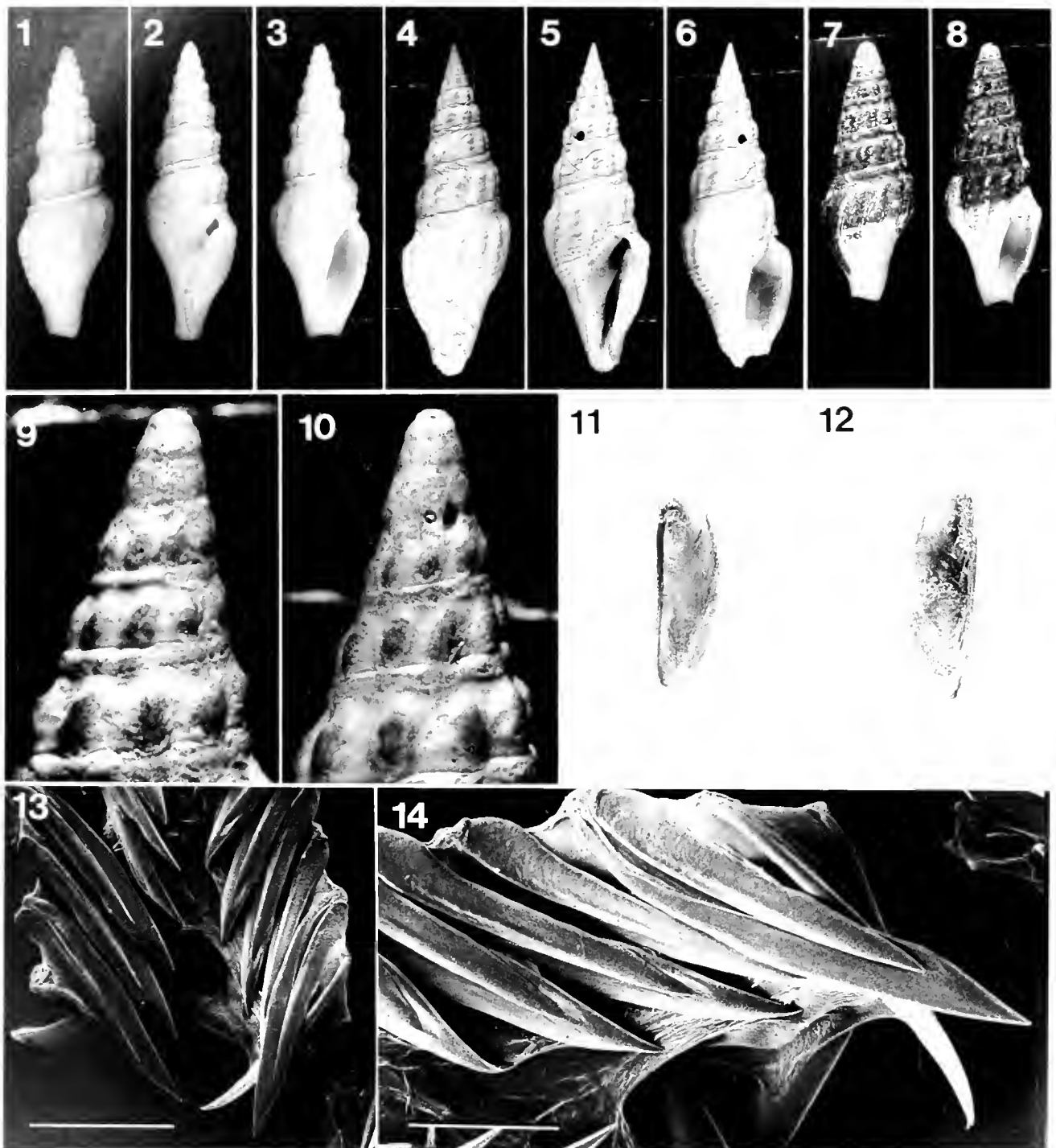
Olsson (1964:98) extended the distribution of the type species to the Esmeraldas formation of Ecuador, from which sediments he also described five additional species of *Buridrillia*. He allocated the genus to “Drillinae” as then understood, which predated the proposal of Crassispirinae.

In his revision of turrid classification, Powell (1966: 62) assigned *Buridrillia* to the Borsoniinae, evidently based on the prominent columellar plication of the type species. However, the radular tooth of the new species *B. deroyorum* is clearly of the duplex (terminology of Morrison, 1966) or modified wishbone type, comparable to that illustrated by Kantor and Taylor (1991, fig. 2B) for *Clinella sinuata* (Born, 1778). This tooth type is characteristic of (but not limited to) the Crassispirinae (McLean, 1971; McLean in Keen, 1971). It is substantially different from the long hollow tooth of the Borsoniinae.

Shell characters other than the columellar plication of *Buridrillia* are reminiscent of the crassispirine genera *Crassispira* (*Crassispira*) Swainson (1840:152, 313), and *Hindsiclava* Hertlein & Strong (1955:227), in which there is a subsutural cord on the smooth shoulder, a deep sinus on the concave shoulder, and axial and spiral sculpture on the body whorl. The columellar plication of *Buridrillia* is evidently convergent with that of Borsoniinae. Assignment of the genus to Crassispirinae is supported both on radular characters and the balance of shell characters.

Buridrillia deroyorum new species
(figures 1–14)

Description: Shell sturdy, fusiform, attaining 57+ mm in length. Spire acuminate, whorls shouldered, shoulder concave, with prominent subsutural cords; axial sculpture of nodose ribs; spiral sculpture of depressed lirae that decussate the axial ribs to form three rows of nodules;



Figures 1-14. *Buridrillia deroyorum* new species. 1-3. Holotype, AMNH 232163, 4-6. Paratype #8, LACM 2461, 7, 8. Paratype #5. AMNH 232165 (Figures 1-8, slightly reduced, see Table 1 for measurements). 9, 10. Paratype #8, LACM 2461, spire enlarged about $\times 2.5$. 11, 12. Paratype #10. Operculum, 11. View of interior side, 12. View of exterior side (Figures 11, 12, about $\times 2.5$). 13, 14. Paratype #12. Radular dentition (Scale bar for 13 = 100µm, for 14 = 50µm).

body whorl with numerous spiral lirae that interrupt the axial sculpture on the anterior half. Protoconch lost on 14 of the 15 specimens, protoconch poorly preserved on paratype #8 (Table 1), of 2 1/2-2 apparently smooth whorls

(Figures 9, 10); body whorl sculptured with 12 to 13 axial ribs. Aperture large, outer lip thin, inflated, explaned with a deep, U-shaped anterior notch, posterior notch deep, widely open; columella with a prominent plication

Table 1. *Buridrillia deroyorum* new species. Shell measurements in mm. Spires not preserved, except for paratype #8. Number of specimens examined = 15

	Length	Width	# Whorls
AMNH 232163			
Holotype	50.1	17.8	7½
AMNH 232164			
Paratype #1	34.4	13.7	5½
Paratype #2	34.2	13.0	5½
Paratype #3	25.7	10.5	5½
AMNH 232165			
Paratype #4	52.4	18.7	7½
Paratype #5	45.5	17.1	6½
Paratype #6	31.0	16.1	6½
Paratype #7	24.3	10.7	6
LACM 2461			
Paratype #8	57.3	19.4	9½
Paratype #9	56.1	18.8	7½
*Paratype #10 (operculum)	48.9	17.3	7½
Paratype #11	35.8	13.1	7½
*Paratype #12 (radula)	22.4	9.8	6½
Paratype #13	15.2	6.4	5½
Paratype #14	12.3	5.1	5
Range	12.3–57.3	5.1–19.4	
Mean	34.4	13.7	

* Specimens providing radula and operculum for photography.

on the proximal part of the pillar. Periostacum dense, flaky, greenish-brown. Shell color buff with light tan bands in the subsutural area and across base; aperture glossy white, tinged with tan. Operculum, small, thin, light brown, long ($H=7.9$ mm) and narrow ($W=2.6$ mm) with a marginal ridge and a terminal nucleus (Figures 11, 12). Radula of both rows of marginal teeth only, of the duplex or modified wishbone type (Figures 13, 14).

Type locality: North of Isla Floreana [also known as Santa Maria Island or Charles Island] 1°14'S, 90°26'W, Galapagos Islands, Ecuador in 310 m, dredged by the DeRoys, April 15, 1979.

Specimens examined: (All dredged by A. and J. DeRoy, in the Galapagos Islands, see Table 1 for measurements): Holotype AMNH 232163 (Figures 1–3) and paratypes 1–3, AMNH 232164, from the type locality; paratypes 4–7, AMNH 232165, from the type locality, May 15, 1978, in 310 m; paratypes 8–14; LACM 2461, off Isla Duncan [0°25'S, 90°43'W] in 365 m, March, 1979.

Distribution: Known only from the Galapagos Islands from the type locality and off Isla Duncan, in 310 and 365 m.

Remarks: Of the five known Neogene species of *Buridrillia* from the Esmeraldas formation described by Olsson (1964), *B. deroyorum* most resembles the type species, *B. panarica*, from the Pliocene of Pacific Panama (type locality) and Costa Rica (Charco Azul formation) as well as from the Pliocene of Ecuador (Esmeraldas formation). The two species are of similar size and have a similar, well-developed columellar plication. From *B. panarica* it differs in having a raised subsutural cord rather than a constricted subsutural band, and in having much more strongly nodose axial ribs.

The columellar plication of *B. deroyorum* is present on all fifteen specimens regardless of size. However, the strength of its continuation on the internal pillar may differ. A strong plication is visible through a hole on the back side of paratype 10 made to extract the radula. However, the pillar in Paratype 8 (Figures 5, 6), which is visible through a naticid drill hole, has a very faint plication. Similar variation has been noted for fossil species of *Buridrillia*. Olsson (1964:98) pointed out that some specimens of the type species have a well-marked columellar fold, but that others lack it or have slight swellings or raised lines. Other species described by Olsson have poorly marked folds or lack folds.

The present distribution of *Buridrillia* is that of a relict genus, a survivor in the eastern Pacific at the Galapagos refugium of a turrid group that was once more widely distributed in the New World tropics during the Neogene.

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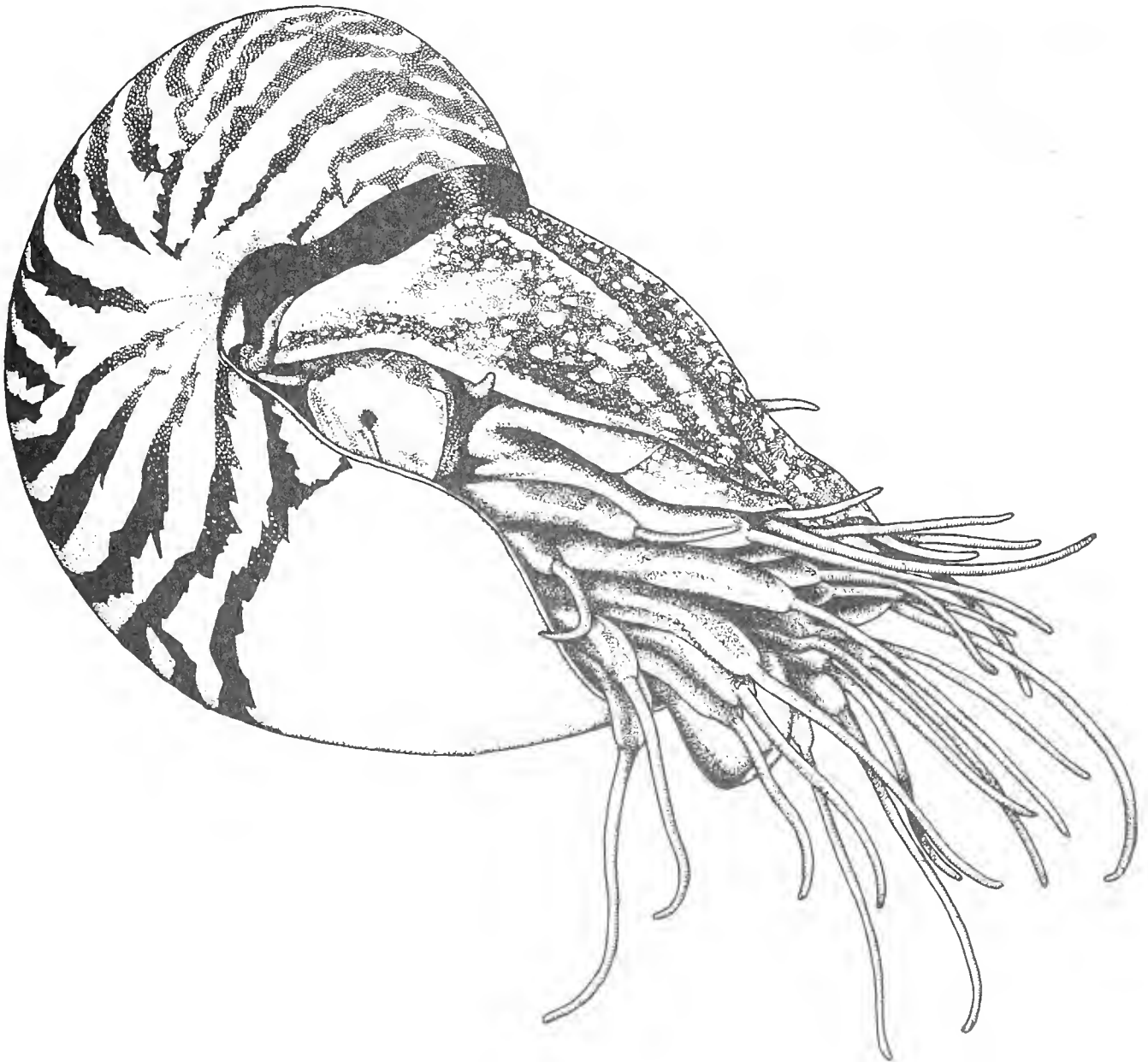
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Notices

58th ANNUAL MEETING OF THE AMERICAN MALACOLOGICAL UNION

The 58th annual meeting of the American Malacological Union will be held August 2-7, 1992, at the Hyatt Sarasota, Sarasota, Florida. Local assistance is being provided by the Sarasota Shell Club and the Mote Marine Laboratory. The meeting will feature contributed papers, bourse and exhibits, a collectors' evening, auction, banquet, and fieldtrips to marine, freshwater, and terrestrial habitats and a nearby fossil pit. Two international symposia are planned: Biology of Caribbean Mollusks, organized by Dr. Rüdiger Bieler [Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, Tel. (312) 922-9410, ext. 270, FAX (312) 663-5397], and Advances in Gastropod Phylogeny, organized by Dr. Terrence M. Gosliner [Department of Invertebrate Biology and Paleontology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, Tel. (415) 750-7277, FAX (415) 750-7090]. Information, registration forms, and a call for papers will be included in the Spring 1992 issue of the AMU Newsletter. Additional information about the meeting and membership applications can be obtained by contacting:

Dr. Robert C. Bullock, President
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WESTERN SOCIETY OF MALACOLOGISTS

The Twenty-fifth Annual Meeting of the Western Society of Malacologists will be held at the Asilomar Conference Grounds on Monterey Bay, Pacific Grove, California, from June 30 to July 3, 1992. In addition to contributed papers on marine, freshwater and terrestrial mollusks, both living and fossil, the agenda includes two special symposia, on Opisthobranchs, and on Cocos Island, Costa Rica. A shell auction, reprint sale, and banquet round out the program. For further information contact WSM President David K. Mulliner (5283 Vickie Drive, San Diego, California 92109; (619) 488-2701) or WSM Treasurer Henry W. Chaney (Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105; (805) 682-4711, ext. 334; fax (805) 569-3170). Deadline for receipt of abstracts is May 15, 1992.

October 11-14, 1992—*Symposium on Freshwater Mussel Conservation and Management*. Embassy Suites Hotel, St. Louis, MO. Sessions devoted to regulations, commercial harvest, conservation, sampling methodology, data management, and environmental awareness. For info: Kurt Welke, Wisconsin Dept. of Natural Resources, 111 W. Dunn St., Prairie du Chien, WI 53821, 608/326-0233

Two New Species of Cancellariidae (Gastropoda: Neogastropoda) from Brazil

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ABSTRACT

Two new species of cancellariids are described from shallow waters of the Brazilian Province. Each has a sister species in the Caribbean Province. *Tritonoharpa leah*, n. sp. differs from *T. lanceolata* in having a more inflated and thinner shell, in which the axial costae are more pronounced than the spiral cords. *Cancellaria petuchi*, n. sp. differs from *C. reticulata* in having a thick, white callus on the columellar side of aperture, a broad, rounded shoulder, and a proportionally longer aperture and larger protoconch than *C. reticulata*. *Cancellaria petuchi* lacks strongly cancellated sculpture on the body whorl and the bifid posteriormost columellar fold of *C. reticulata*.

Key words: Cancellariidae; *Tritonoharpa*, *Cancellaria*; new species, Brazil

INTRODUCTION

The molluscan fauna of Brazil has been regarded by most authors (e.g., Abbott, 1974; Rios, 1970, 1975, 1985) as comprising the southernmost component of the Caribbean Province. Several workers, among them Ekman (1953), Work (1969) and Rios (1970), had commented on an endemic component of the Brazilian molluscan fauna, while others (Briggs, 1974; Coelho & Koenig, 1972; Coelho & Ramos, 1972) had suggested the existence of a Brazilian Subprovince or Province. More recently, Petuch (1988:166) delimited the region extending from the mouth of the Amazon River southward into the Mar de Plata as the Brazilian Province and listed a number of endemic molluscan indicator species. Other authors (e.g., Vokes, 1990) have begun to distinguish between Brazilian species and their often closely related Caribbean counterparts.

The cancellariid fauna of Brazil is poorly known. Lange de Morretes (1949, 1953) did not include any member of this family in his catalogs of Brazilian mollusks, while Abbott (1974:246) and Rios (1970:111, 1975:127, 1985:126) listed only *Cancellaria reticulata* Linné, 1767 and *Tritonoharpa lanceolata* (Menke, 1828) (as *Colubraria lanceolata*) as occurring in the Brazilian fauna. Verhecken (1991) underscored the paucity of records for this

family in the fauna of the subequatorial western Atlantic, and described two bathyal cancellariids from off southeastern Brazil.

A large series of specimens of an undescribed *Cancellaria* as well as two specimens of a new species of *Tritonoharpa* were recently made available to us from commercial and institutional sources. We take pleasure in naming these new species after the persons who first brought them to our attention.

ABBREVIATIONS USED IN TEXT

KBIN—Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels

MINHN—Muséum national d'Histoire naturelle, Paris

MORG—Museu Oceanográfico da Fundação Universidade do Rio Grande, Rio Grande, Brazil.

UFJF—Universidade Federal de Juiz de Fora, Minas Gerais

USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC

SYSTEMATICS

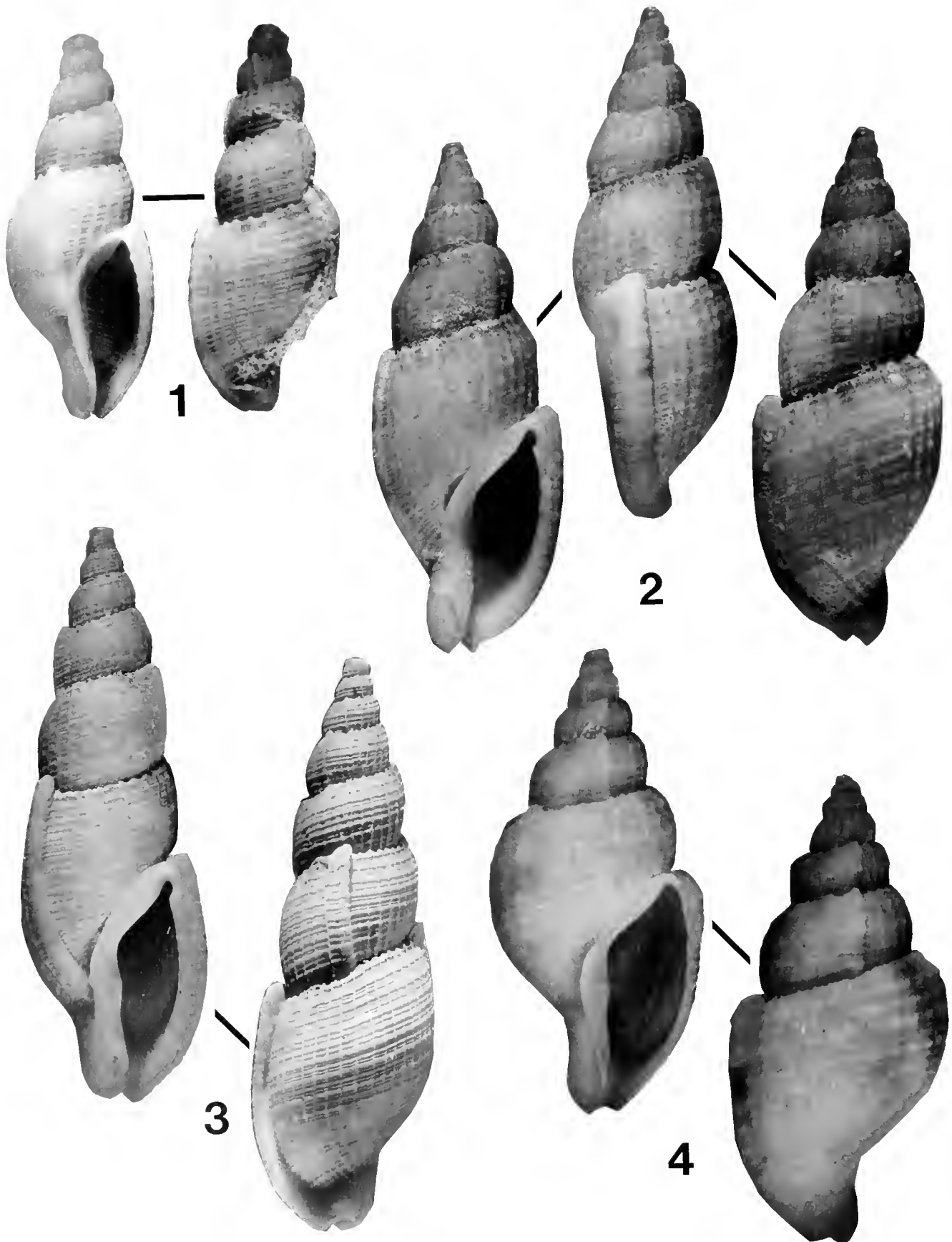
Family Cancellariidae Forbes & Hanley, 1851

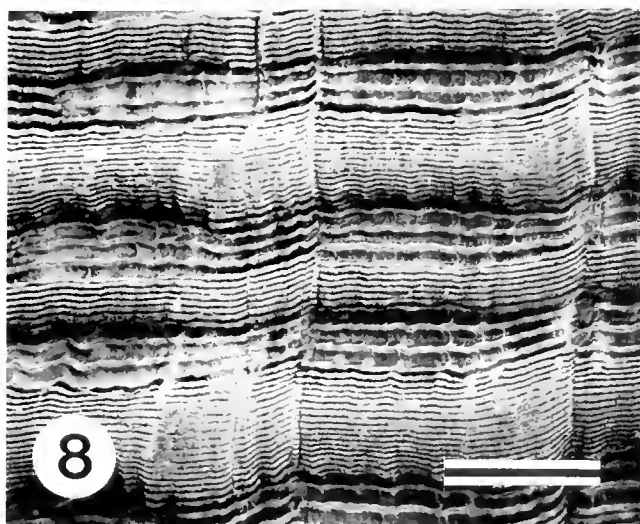
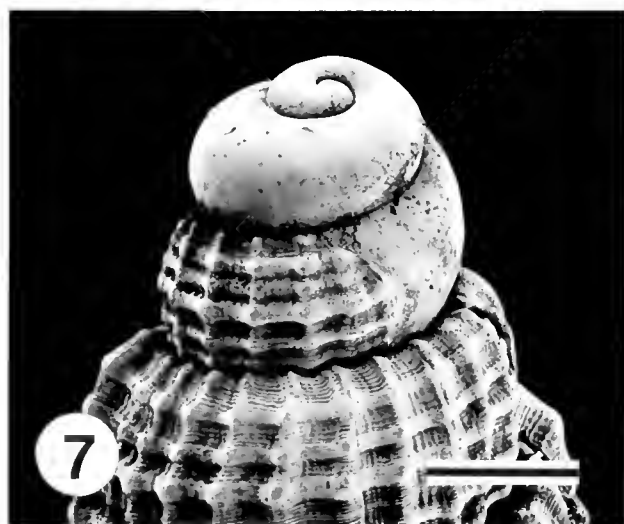
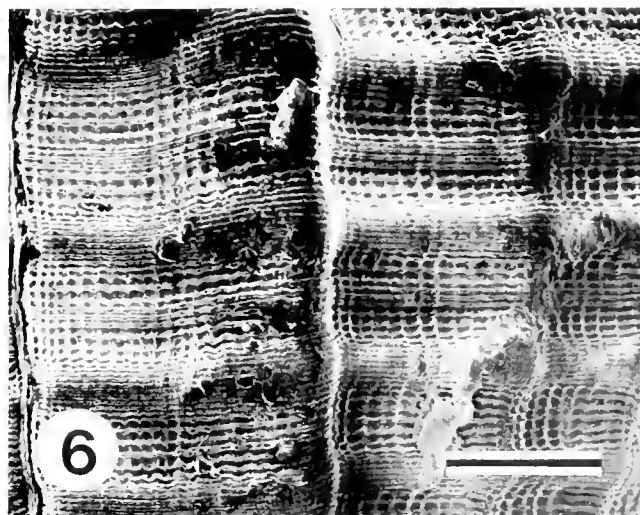
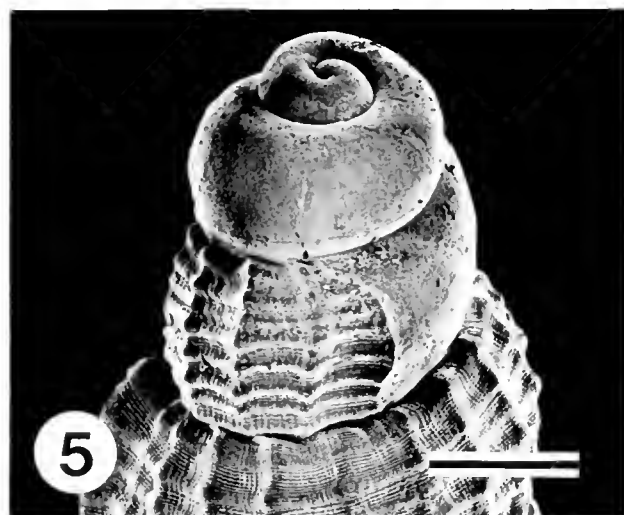
Subfamily Plesiotritoninae Beu & Maxwell, 1987

Genus *Tritonoharpa* Dall, 1908

Beu and Maxwell (1987) reviewed the genus *Tritonoharpa*, enumerating the following diagnostic characters: elongate-ovate to biconic shells with spire half or more the shell length; weakly to moderately convex teleoconch whorls; prominent non-collabral varices on early as well as later whorls; well developed columellar collar; columellar plait either single and weak or absent; radula absent.

Recent western Atlantic species of *Tritonoharpa* include the Carolinian and Caribbean *T. lanceolata* (Menke, 1828); *T. cubapatriae* (Sarasua, 1975), based on a unique holotype from off Havana, Cuba; *T. bayeri* (Petuch, 1987) from the Caribbean coast of Colombia;





Figures 5–6. *Tritonoharpa leali* new species. 5. Protoconch of holotype, scale bar = 500 μ m. 6. Surface sculpture of holotype, scale bar = 200 μ m. **Figures 7–8.** *Tritonoharpa lanceolata* (Menke, 1828). 7. Protoconch of specimen in figure 3, scale bar = 500 μ m. 8. Surface sculpture of specimen in figure 3, scale bar = 200 μ m.

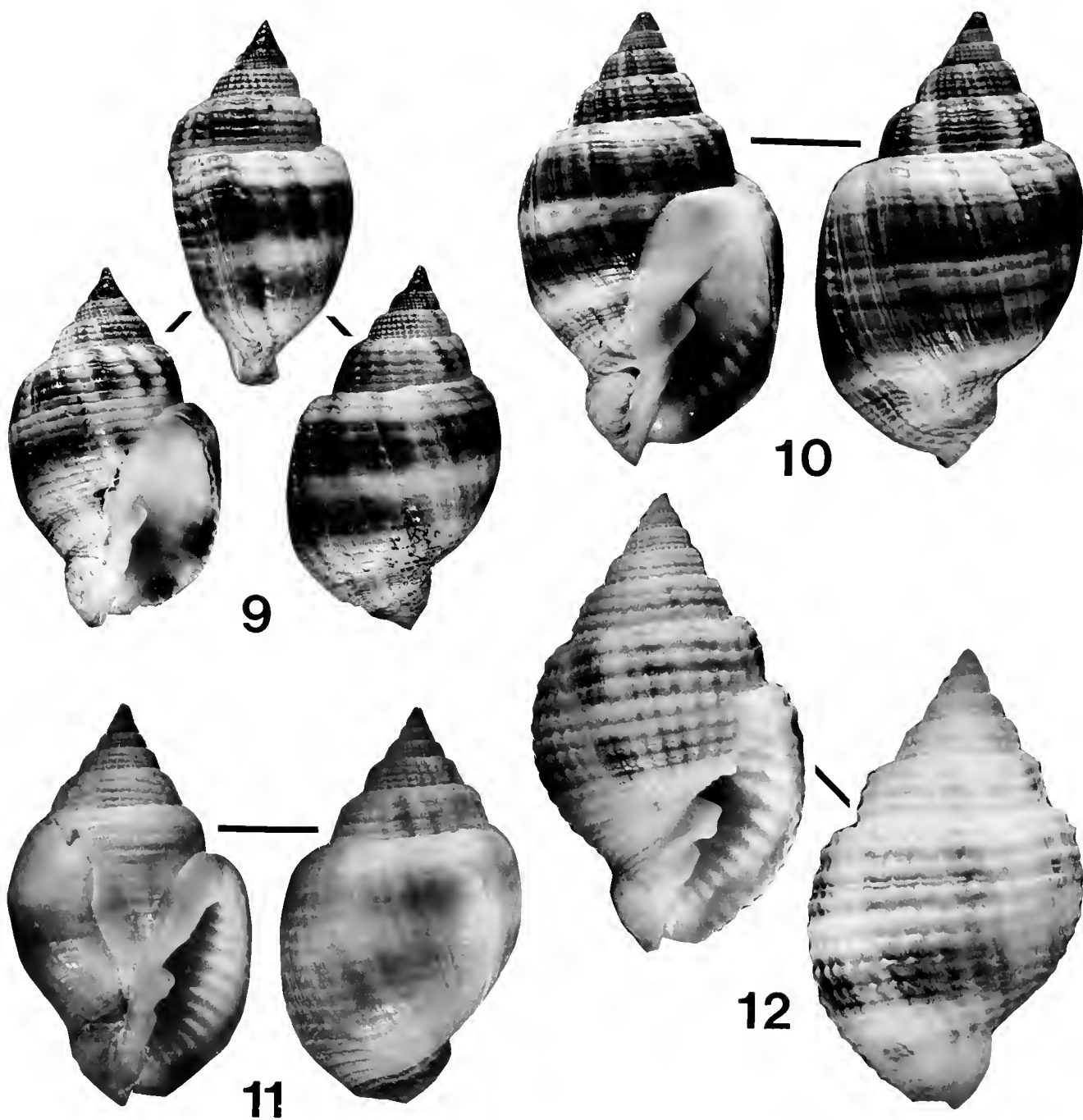
and the new species described below. *Minibraria monroei* (McGinty, 1962) has been referred to the Muricidae on the basis of the morphology of its varices and protoconch (Beu & Maxwell, 1987:56).

Tritonoharpa leali new species
(figures 1, 2, 5, 6)

Description: Shell (figures 1–2) to 18.4 mm, thin, tall, narrow. Spire high (spire angle 31–35°), stepped, comprising about $\frac{3}{5}$ of total shell length. Protoconch paucis-

piral, of $2\frac{1}{4}$ inflated, weakly shouldered whorls (figure 5). First $1\frac{1}{2}$ whorls nearly planispiral, descending rapidly thereafter. Protoconch coaxial with, or deviated from, teleoconch axis by up to 5°. Transition to teleoconch abrupt, marked by flared protoconch lip and onset of pronounced spiral sculpture. Teleoconch with up to $5\frac{2}{3}$ slightly inflated, weakly shouldered whorls. Suture deeply impressed, obscured by axial costae of succeeding whorl. Spiral sculpture of strong, low, equally spaced cords, 20–26 on body whorl, 12–15 on penultimate whorl; cords, 0–3, weak or absent on siphonal canal. Axial sculp-

Figures 1–2. *Tritonoharpa leali* new species. 1. Holotype, MORG 28659, Davis Bank, southeastern Brazil, 20°40'S, 34°41'W, in 60 m, Marion-Dufresne MD55 sta. DC40, 7.5 \times . 2. Paratype 1, USNM 860521, off Itaparica Island, Bahia, Brazil, trawled in 20 m, 5.0 \times . **Figure 3.** *Tritonoharpa lanceolata* (Menke, 1828). USNM 798073. Off St. Thomas, Virgin Islands, 5.0 \times . **Figure 4.** *Tritonoharpa bayeri* (Petuch, 1987), Holotype, USNM 859853, Cabo La Vela, Goajira Peninsula, Colombia, in 35 m, 5.0 \times .



Figures 9–10. *Cancellaria petuchi* new species. 9. Holotype, MORG 28660, 2.0×. 10. Paratype 4, USNM 859409, Off Vitória, Espírito Santo, Brazil, trawled on sand bottom in 40 m, 2.0×. Figure 11. *Cancellaria adela*e Pilsbry, 1940, USNM 508663, Little Duck Key, Florida, 1.5×. Figure 12. *Cancellaria reticulata* (Linné, 1767), USNM 811479, 30 mi. ENE of Eau Gallie, Florida [28°17'N, 80°01'W], in 34–41 fms (62–75 m), R/V Silver Bay Sta. 2010, 2.0×.

ture of pronounced varices and narrow, opisthocline costae. Varices high, non-collabral, narrow, rounded abaperturally, undercut adaperturally, 180–200° apart on early whorls, up to 238° apart on later whorls. Costae (7–22 between varices, 15–33 per whorl) offset from varices by 5–10°, producing cancellate sculpture at their intersection with spiral cords. Aperture narrow, elliptical, with

well defined posterior notch. Inner lip smooth, with columellar collar reflected over, but not adherent to, fasciole and pseudoumbilicus. Outer lip with up to 8 pairs of denticles confined to flared region beyond varix. Siphonal canal short, dorsally reflected, partially covered abaxially. Base color khaki to yellowish tan, with darker brown maculations anterior to suture and along varices.

Table 1. Shell measurements of *Cancellaria reticulata* and *C. petuchi*. All measurements in mm (N = 10). For *C. reticulata*, the 10 specimens were selected from throughout the species range, while for *C. petuchi*, data is based on specimens from a single lot (paratypes 4–13).

	<i>C. reticulata</i>		<i>C. petuchi</i>	
	\bar{x}	σ	\bar{x}	σ
Shell length (SL)	39.67	6.21	33.68	1.98
Aperture length (AL)	25.64	3.99	23.64	1.33
(AL/SL)	0.65	0.03	0.70	0.01
No. whorls, teleoconch	6.34	1.76	5.51	0.20
No. whorls, protoconch	2.67	0.10	2.74	0.06
Diameter, protoconch	1.23	0.06	1.60	0.05
Diameter, no. whorls, protoconch	0.46	0.02	0.59	0.02

Type locality: Davis Bank, southeastern Brazil, 20°40'S, 34°41'W, in 60 m, Marion-Dufresne MD55 sta. DC40, May 1987.

Material examined: Holotype, MORG 28659, 9.22 mm; Paratype 1, USNM 860521, off Itaparica Island, Bahia, Brazil, trawled in 20 m, 18.44 mm.

Distribution: This species is known from two records, both off the state of Bahia, Brazil, in depths of from 20 to 60 m.

Etymology: This species honors Dr. José H. Leal, in recognition of his contributions to the study of Brazilian mollusks.

Comparative remarks: *Tritonoharpa leali* most closely resembles *T. lanceolata*, from which it differs in having a somewhat more inflated and thinner shell, in which the axial costae are more pronounced than the spiral cords (compare figures 5 and 7). *Tritonoharpa bayeri* is even broader and thinner than *T. leali*, and is the only western Atlantic *Tritonoharpa* in which the aperture length exceeds half the shell length.

Subfamily Cancellariinae Forbes & Hanley, 1851

Genus *Cancellaria* Lamarck, 1799

The genus *Cancellaria* is characterized by the presence of a thick, ovate to biconic shell with strongly cancellate sculpture, prosocline outer lip, a weak stromboid notch, short but distinct siphonal canal, prominent siphonal fasciole, lirate outer lip, and columella with two to three strong folds, the posteriormost strongest and usually bifid.

Jung and Petit (1990:100) reduce *Pyruchia* Olsson, 1932 to subgeneric status within *Cancellaria*, and distinguish it from the nominotypical subgenus on the basis of its pyriform shape with reduced or absent sculpture on body whorl and a columella with two strong, non-bifid folds.

Cancellaria petuchi new species

(figures 9, 10, 14–16)

Description: Shell (figures 9–10) to 37 mm, heavy biconic, pseudumbilicate. Spire high (spire angle 62–70°), conical, comprising about 2/3 of total shell length. Protoconch paucispiral, of 2½ low, inflated, glassy whorls

(figure 14). Protoconch may be co-axial with, or deviated from teleoconch axis by up to 15°. Teleoconch with up to 6½ strongly convex whorls. Suture deeply impressed. Spiral sculpture of 18–24 major cords on body whorl, 6–10 on siphonal canal, 6–8 on penultimate whorl. Axial sculpture of 20–38 prosocline ribs that form strongly cancellate sculpture at intersection with spiral cords, especially on first four teleoconch whorls. Thereafter, axial ribs become broader, less pronounced, may disappear entirely, especially below the shoulder. Aperture large, broad, hemi-elliptical, deflected from coiling axis by 12–18°. Outer lip with shallow indentation posterior to junction with siphonal canal and 10–12 strong lirae, slightly recessed, either diminishing ¼ whorl into aperture, or more usually, disappearing and reappearing ¼ whorl within the aperture. Inner lip with 2 columellar and 1 siphonal folds. Posteriormost columellar fold largest, overlying siphonal fasciole. All folds with single, sharp keel. Siphonal canal short, deflected dorsally and abaxially. Base color white to light tan, with spiral bands of base color, especially on early whorls. Some specimens pure white. Aperture with white overglaze forming thick callus along columella.

Type locality: N.E. of Vitória, Espírito Santo, Brazil, 19°35'S, 39°42'W, in 15 m. South Eastern Brazil N.O. Marion-Dufresne MD55 sta. DC87, May 1987.

Material examined: Holotype, MORG 28660, 28.16 mm; Paratypes 1–3, MNHN, N.E. of Vitória, Espírito Santo, Brazil, 19°34'S, 39°34'W, in 34 m, N.O. Marion-Dufresne MD55 sta. CB90, May 1987, 32.52 mm, 11.01 mm, 8.06 mm; Paratypes 4–23, USNM 859409, Paratypes 24–36, Petit collection, Paratypes 37–38, KBIN, Paratypes 39–52, Verhecken collection, all from Off Vitória, Espírito Santo, Brazil, trawled on sand bottom in 40 m, 29.26–36.56 mm. Paratypes 53–55, Petit collection, Mangue da Olaria, Guarapari, Espírito Santo, Brazil, in sand, minus tide. Paratypes 56–57, UFJF, Niterói, Rio de Janeiro, Brazil. Paratype 58, MORG 19472, off Salinópolis, Pará, Brazil, in 36 m. Paratypes 59–62, MORG 23307, Coroa Vermelha, Abrolhos Islands, Bahia, Brazil, in 1 m.

Distribution: This species ranges from off Salinópolis, Pará, to off Niterói, Rio de Janeiro, Brazil. It occurs from intertidal depths to 40 m.

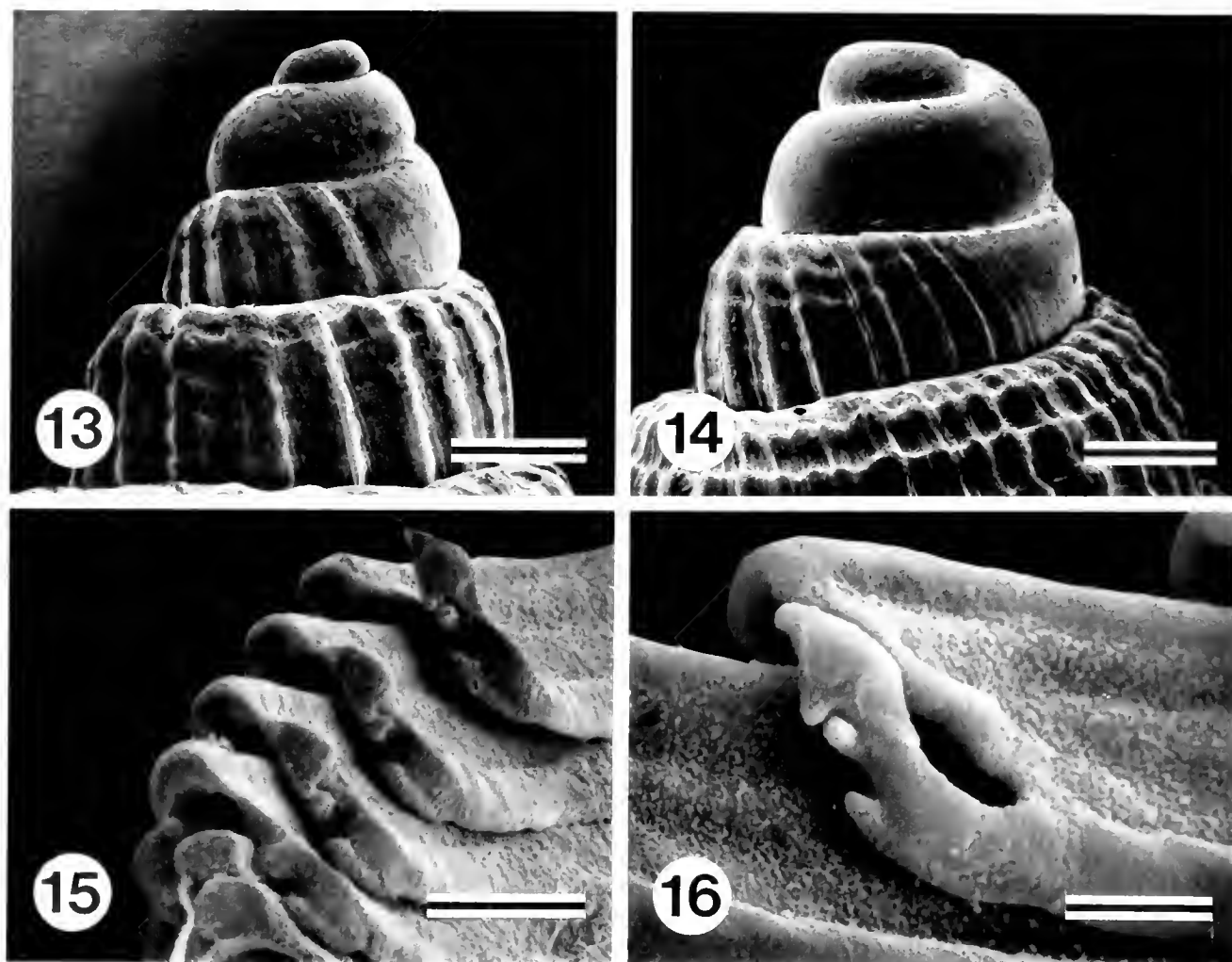


Figure 13. *Cancellaria reticulata* (Linné, 1767). Protoconch, scale bar = 500 μ m. **Figure 14–16.** *Cancellaria petuchi* new species. **14.** Protoconch of paratype, same data as fig. 10. Scale bar = 500 μ m. **15.** Frontal and **16.** Lateral view of distal ends of radicular teeth. Scale bars = 5.0 μ m (fig. 15), 3.0 μ m (fig. 16).

Etymology: This species honors Dr. Edward J. Petuch, as a tribute to his contributions to our knowledge of the molluscan fauna of Brazil, and the Neogene zoogeography of the western Atlantic faunas.

Comparative remarks: *Cancellaria petuchi* differs from its geographically proximate congener *C. reticulata* in having reduced or absent cancellate sculpture on the body whorl and lacking a bifid posteriormost columellar fold. *Cancellaria petuchi* has a thick, white callus on the columellar side of the aperture and a broad, rounded shoulder, features lacking in *C. reticulata*. *Cancellaria petuchi* also has a proportionally longer aperture and larger protoconch than *C. reticulata* (table 1). Radular morphology of *Cancellaria petuchi* (figures 15, 16) agrees in all essential features with that of *C. reticulata* (Harsen & Petit, 1982: figures 14, 15—these figures show the ventral surfaces of the distal tips of two radular teeth).

Of the western Atlantic species of *Cancellaria*, *C. petuchi* most strongly resembles *C. adelae* Pilsbry, 1940

(figure 11), a species endemic to the Florida Keys, with which it shares its predominantly smooth body whorl sculpture and thick parietal overglaze. *Cancellaria adelae* however, has a strongly bifid columellar fold, and indeed, may have an additional fold along the posterior portion of columella.

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New Species of *Solariella* (Gastropoda: Trochidae) from the Western Atlantic Ocean

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ABSTRACT

Three new species of the genus *Solariella* Wood, 1842, are described. *Solariella quadricincta* is known only from the continental shelf off northeastern Venezuela in depths of 26–86 m, and *S. staminea* is known only from the Davis Seamount off southeastern Brazil in 60 m; shells of both species are very similar to those of *S. carvalhoi* Lopes and Sá Cardoso, 1958. *Solariella cristata* is known from the upper continental slope of Isla Cancun, Yucatán, Mexico, and off Key Largo, Florida Keys, in depths of 155–256 m, and off St. Vincent, Lesser Antilles in 165–201 m.

Key words: Trochidae; Solariellinae; *Solariella*; systematics; new species.

INTRODUCTION

Two recent monographs of western Atlantic Trochidae present accounts of the faunas of restricted geographical areas: the Straits of Florida (Quinn, 1979) and the Gulf of Mexico (Quinn, in press). In the process of examining specimens for those reports, several new species from other areas of the western Atlantic Ocean were discovered. This paper presents descriptions of three new species of *Solariella* Wood, 1842. These species are included in *Solariella* because of the similarities of their shells to those of species such as *S. lacunella* (Dall, 1881); however, because radular characters are important (Herbert, 1987) and animals of the three species were unavailable for study, such assignment of these species is tentative at present.

Institutional abbreviations used in this paper are as follows: MNHN (Museum National d'Histoire Naturelle, Paris, France); MORC (Museu Oceanográfico da Fundação Universidade do Rio Grande, Rio Grande, RS, Brazil); UMML (Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida); USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

SYSTEMATICS

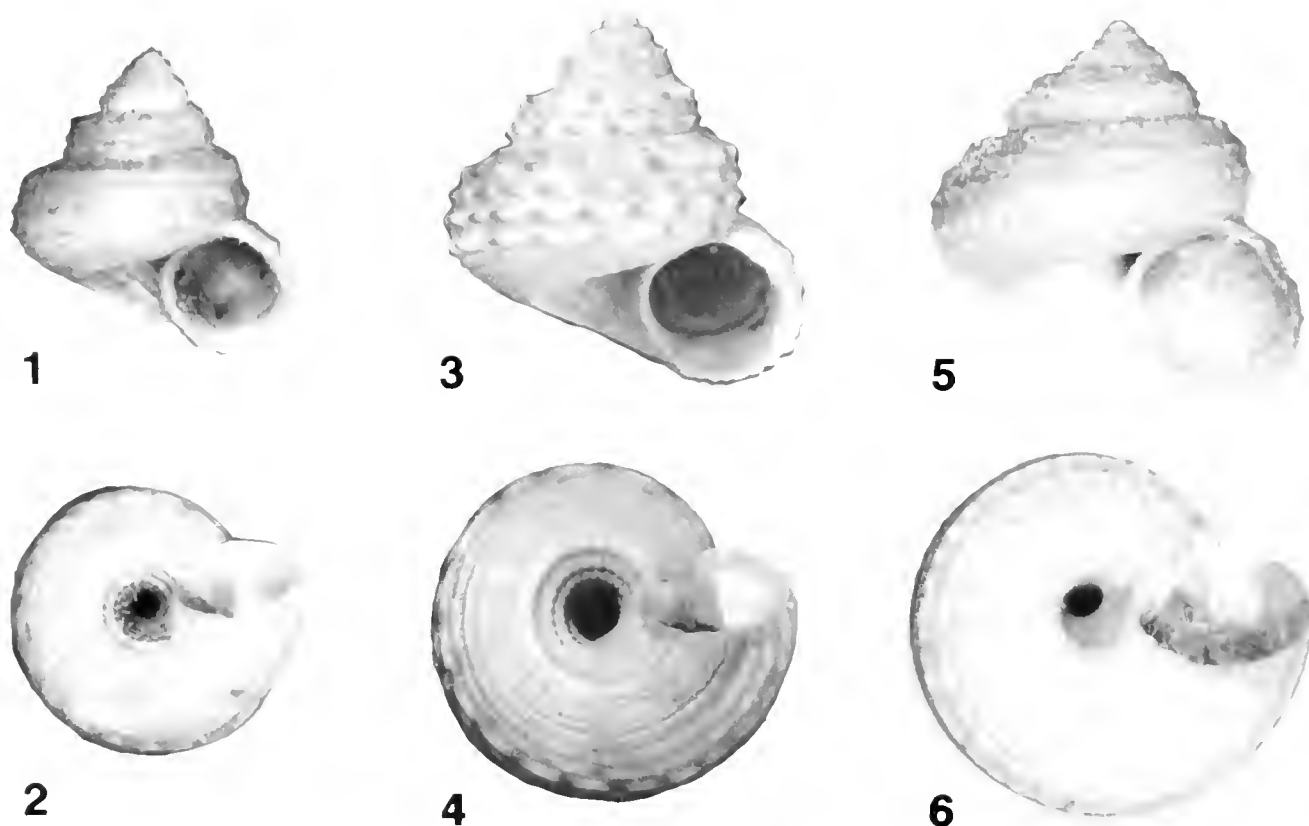
Genus *Solariella* Wood, 1842

Type species (monotypy): *Solariella maculata* Wood, 1842.

Solariella quadricincta new species
(figures 1–4)

Material examined: 1 fragment, UMML 30.6695 (paratype); JOHN ELLIOTT PILLSBURY Station P-727, 10°20'N, 65°02'W, 64 m; 10-ft otter trawl; 21 July 1968.—1 specimen, UMML uncatalogued [examined and photographed in 1975 (figs. 3, 4), but a recent attempt to relocate this specimen was unsuccessful, and it is presumed lost]; JOHN ELLIOTT PILLSBURY Station P-721, 11°06.5'N, 64°22.5'W, 26–27 m; 10-ft otter trawl; 21 July 1968.—1 specimen, USNM 859437 (holotype); 1 specimen, UMML 30.6528 (paratype); JOHN ELLIOTT PILLSBURY Station P-718, 11°22.5'N, 64°08.6'W, 60 m; 10-ft otter trawl; 20 July 1968.—1 specimen, UMML 30.6376 (paratype); JOHN ELLIOTT PILLSBURY Station P-705, 10°45'N, 62°00'W, 77–86 m; 10-ft otter trawl; 18 July 1968.

Description: Shell of moderate size for genus, attaining 6.55 mm height, 7.15 mm width, umbilicate, ivory with light orange-brown spots and flammules, nacreous under thin outer porcelainous layer. Protoconch 300–325 μ m maximum diameter, of about 1 whorl. Teleoconch whorls 5.5, tubular, shouldered; first 3 whorls with 3 strong, subequal spiral cords forming whorl periphery, adapical cord forming whorl shoulder; subsequent whorls with subsutural spiral cord forming narrow channel with suture; last whorl with fourth primary spiral cord, subequal to other peripheral spiral cords and coincident with suture on previous whorls; 1–2 weak spiral cords sometimes occurring between primary spiral cords; fine spiral threads overlying interspaces and primary spiral cords on last 3 whorls. Axial sculpture consisting of rather strong riblets on whorls 2 and 3, fading in strength to numerous colabral threads in interspaces of spiral cords on subsequent



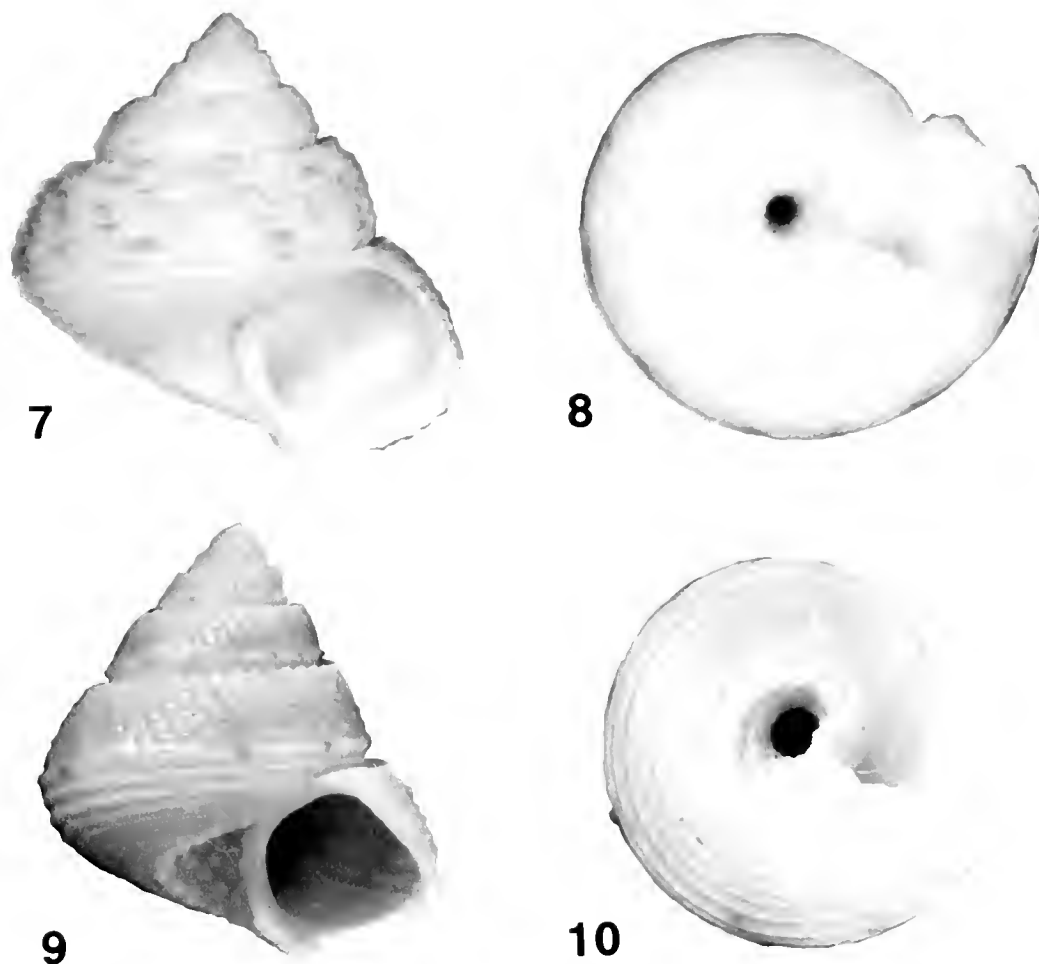
Figures 1–4. *Solariella quadricincta* new species. **1, 2.** Apertural and basal views of holotype, USNM 859437, height 6.40 mm, width 6.40 mm, from off Isla de Margarita, Venezuela, 11°22.5'N, 64°08.6'W, 60 m. **3, 4.** Apertural and basal views of specimen (lost, measurements unknown), UMML 30.6639, from off Isla de Margarita, Venezuela, 11°06.5'N, 64°22.5'W, 26–27 m. **Figures 5, 6.** *Solariella carvalhoi* Lopes and Sá Cardoso, 1958. FSBC 139514, height 7.9 mm, width 8.2 mm, from Cagaras Island, Rio de Janeiro, Brazil, 32 m.

whorls; axial threads form lamelliform beads on subsutural spiral cord, weakly beading shoulder spiral cord on whorls 3–5. Subsutural shelf rather wide, flat, sloping abapically from subsutural spiral cord to shoulder spiral cord; fine spiral threads appearing on third whorl near shoulder, progressively covering shelf surface on subsequent whorls; 1–2 stronger spiral threads appearing on last whorl. Base convex, with 6–7 strong spiral cords; cords and interspaces with fine spiral threads; interspaces with fine collabral threads. Umbilicus wide, about 40–45% maximum shell width, funnel-shaped; walls convex, with 6 strongly beaded spiral cords. Shell ground color ivory, with regularly spaced, spirally elongate light orange-brown spots on major spiral cords, with occasional flammules of same color on subsutural shelf. Operculum thin, corneous, multispiral.

Type locality: Off Isla de Margarita, Venezuela, 11°22.5'N, 64°08.6'W, 60 m.

Remarks: Shells of *Solariella quadricincta* closely resemble those of *S. staminea*, new species, and *S. carvalhoi* Lopes and Sá Cardoso, 1958, from Brazil (figs. 5, 6). Shells of all three species have four strong, subequal

primary spiral cords on the last whorl, of which the shoulder spiral cord is the most distinctly beaded; have fine spiral threads on suprabasal whorl surface; and have flat subsutural shelves. Shells of *S. quadricincta* differ from those of *S. staminea* by being slightly narrower (height:width ratios = 0.92–1.01 and 0.79–0.90, respectively); by having a channeled suture; by having crisp rather than flattened axial threads; by having fewer, narrower, rounded basal spiral cords; by having a narrow and more strongly beaded circumumbilical cord; by having more numerous, more strongly beaded intra-umbilical spiral cords; and by having a strong, distinct color pattern. Shells of *S. quadricincta* differ from those of *S. carvalhoi* by being smaller at similar whorl number; by having canaliculate sutures; by having more steeply sloping subsutural shelves; by having finer, crisper, more closely spaced axial threads that are present in the interspaces of all spiral cords; by having a more finely beaded shoulder cord; by having wider interspaces between the basal spiral cords; and by having more strongly beaded intraumbilical spiral cords. *Solariella quadricincta* is only known from the continental shelf off north-eastern Venezuela in depths of 26–86 m.



Figures 7–10. *Solariella cristata* new species. **7, 8.** Holotype, USNM 859421, height 9.1 mm, width 9.45 mm, from SE of St. Vincent, Lesser Antilles, 13°11.2'N, 61°05.1'W, 165–201 m. **9, 10.** Paratype, UMML 30.5669, height 8.1 mm, width 8.0 mm, from off Isla Mujeres, Yucatán, Mexico, 21°07'N, 86°21'W, 155–205 m.

Solariella cristata new species
(figures 7–10)

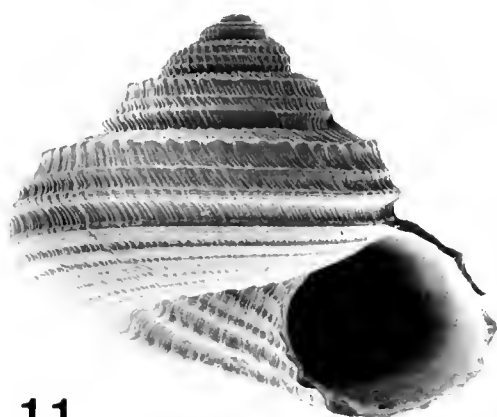
Material examined: 1 specimen, UMML 30.5669 (paratype); JOHN ELLIOTT PILLSBURY Station P-598, 21°07'N, 86°21.0'W, 155–205 m; 10-ft otter trawl; 15 March 1968.—1 specimen, UMML 30.7433 (paratype); GERDA Station G-61, 25°14'N, 80°02'W, 256 m; 6-ft otter trawl; 29 August 1962.—1 specimen, USNM 859421 (holotype); JOHN ELLIOTT PILLSBURY Station P-874, 13°11.2'N, 61°05.1'W, 165–201 m; 5-ft Blake trawl; 6 July 1969.

Description: Shell rather large for genus, attaining 9.1 mm height, 9.45 mm width, umbilicate, ivory with light brown spots and flammules, nacreous under thin outer porcelainous layer. Protoconch 300–320 μ m maximum diameter, of about 1 whorl. Teleoconch whorls 6.1, tubular, shouldered; first 3 whorls with 4–5 spiral cords, increasing to 14 on body whorl; abapical cord on whorls 3–5 strongest, forming peripheral carina; cords on last whorl becoming subequal to peripheral cord, giving whorl

more evenly rounded appearance. Axial sculpture appearing on whorl 2, consisting of rather strong, low, flattened folds on adapical half to two-thirds of whorls 2–4, becoming narrower, rounded, more crowded, and extending to level of suture on subsequent whorls; axial folds forming strong, rounded beads on spiral cords, beads strongest on adapical part of whorl. Subsutural shelf narrow, sloping adapically from suture to shoulder spiral cord; single strong spiral cord bisecting shelf. Base weakly convex, with 7–10 strong, smooth spiral cords. Umbilicus wide, about 30% maximum shell width, funnel-shaped; walls convex, with 4–6 strong, strongly beaded spiral cords. Shell ground color ivory, with scattered light brown spots appearing on fourth whorl, becoming more numerous and forming irregular axial flammules on last whorl.

Type locality: SE of St. Vincent, Lesser Antilles, 13°11.2'N, 61°05.1'W, 165–201 m.

Remarks: The peripherally carinate, rather strongly axially sculpted shells of *Solariella cristata* most closely



11



12

Figure 11–12. *Solariella staminea* new species. Apertural and basal views of holotype, MORC 26530, height 3.8 mm, width 4.8 mm, from Davis Seamount, Brazil, 20°40'S, 34°41'W, 60 m

resemble shells of *S. cincta* (Philippi, 1836) (see Fretter & Graham, 1977:46–48, figs. 31, 32) from the north-eastern Atlantic Ocean. However, shells of *S. cristata* are larger, have a narrower subsutural shelf, and have a distinct color pattern, whereas those of *S. cincta* are uniformly ivory. The only other western Atlantic species having shells with a strongly carinate periphery is *S. patriac* Carcelles, 1953, but shells of that species lack other spiral cords except the shoulder and circumbasal spiral cords, and have only three basal cords (see Rios, 1985:23, pl. 10, fig. 97). The three widely separated localities from which *S. cristata* has been collected (the Florida Keys, Yucatán, and the Lesser Antilles) suggest that the species is widespread, but rare, in the Caribbean Sea.

Solariella staminea new species
(figures 11, 12)

Material examined: 1 specimen, MORC 26530 (holotype); 3 specimens, MNHN uncatalogued (paratypes); MARION-DUFRESNE Cruise MD-55, Station DC-40, 20°40'S, 34°41'W, 60 m; dredge; May 1987; P. Bouchet, J. H. Leal, and B. Metivier collectors.

Description: Shell of moderate size for genus, attaining 6.7 mm height, 7.45 mm width, umbilicate, white with few light yellow to orange-brown spots and streaks, nacreous under thin outer porcelaneous layer. Protoconch about 300 μ m maximum diameter, of about one whorl. Teleoconch whorls 5.6, tubular, shouldered; spire whorls with 3 strong spiral cords, adapical one forming whorl shoulder; last whorl with fourth strong spiral cord, subequal to other spiral cords and coincident with suture on previous whorls; 1–2 additional, weaker, intercallary spiral threads sometimes present; fine spiral threads overlying interspaces and lower 2–3 spiral cords on last 3 whorls. Axial sculpture of rather strong riblets on whorl 2, fading in strength to numerous, crowded, rather flattened collabral threads in interspaces of spiral cords on subsequent whorls; axial threads forming weak, rounded

beads on shoulder spiral cord, finely beading other spiral cords. Subsutural shelf moderately wide, flat, sloping abapically from suture to shoulder spiral cord; fine spiral threads appearing on third whorl; one spiral cord appearing near beginning of first whorl, but fading to obscure angulation or disappearing on second whorl; 1–2 spiral cords appearing on third whorl, one near middle of shelf strongest. Base weakly convex, with 9–11 strong, flattened spiral cords; innermost cord strap-like and weakly beaded; interspaces with fine collabral threads, forming weak rugae on spiral cords on adaxial half of base. Umbilicus wide, about 35–45% maximum shell width, funnel-shaped; walls convex, with 4–5 beaded spiral cords. Shell ground color white, with few, widely spaced light yellow to orange-brown spots, principally on shoulder cord, but occasionally extending abaxially as short streaks or flammules.

Type locality: Davis Seamount, off southeastern Brazil, 20°40'S, 34°41'W, 60 m.

Remarks: Shells of *Solariella staminea* are very similar to those of *S. quadricincta* and *S. carvalhoi*. Differences that distinguish shells of *S. staminea* from those of *S. quadricincta* are discussed in the Remarks section of the latter species. Shells of *S. staminea* differ from those of *S. carvalhoi* by being broader (height:width ratios = 0.79–0.90 and 0.93–0.98, respectively); by having a broader subsutural shelf with stronger spiral cords and axial threads; by having a shoulder spiral cord bearing rounded rather than spirally elongate beads; by having more numerous, flatter basal spiral cords; by having a circumumbilical spiral cord that is broad, flat, and weakly beaded rather than narrow, sharp, and strongly beaded; by having stronger, more weakly beaded intraumbilical cords; and by having a very weak color pattern.

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for access to the collections under his care and for permission to describe the new species in that material. The late Joseph Rosewater and Richard S. Houbbrick (both USNM) kindly allowed me to examine types and other material. José H. Leal brought the specimens of *Solariella staminea* to my attention and kindly provided the SEM micrographs of that species. Eliezer de C. Rios (MORG) generously provided comparative material of *Solariella carvalhoi*. Marjorie Myers, Llyn French, and Judy Leiby provided valuable word-processing and editorial assistance. Thomas H. Perkins and William G. Lyons (both Department of Natural Resources, Florida Marine Research Institute), and two anonymous reviewers provided valuable critiques of previous drafts of this paper.

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A New Fossil Land Snail of the Genus *Hemitrochus* from Bowden, Jamaica¹

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ABSTRACT

A new species of *Hemitrochus*, *H. bowdenensis*, is described from a collection made in the Bowden Beds at Bowden, Jamaica. The species differs from its nearest relative *H. graminicola* (the only modern *Hemitrochus* found in Jamaica) on the basis of shell sculpture, the shape of the whorls, and umbilical width. Analysis of amino acid D/L ratios from one specimen indicates a late Holocene age for the sample and that therefore the material does not belong stratigraphically to the Bowden Beds (of early Pliocene age). The species is apparently extinct, probably as a result of either habitat destruction following European settlement or late Holocene climatic changes.

Key words: land snail, fossil, new species, Jamaica, *Hemitrochus*, Bowden.

INTRODUCTION

The Bowden Beds, located near Bowden, St. Thomas Parish, in southeastern Jamaica, have yielded an extremely rich marine mollusk fauna (Woodring, 1925, 1928) as well as a number of land snails, including a species of helicimid of the genus *Lucidella* (Simpson, 1895), three species of poteriids (Simpson, 1895; Bartsch, 1942; Morrison, 1955), and two species of camaenids of the genus *Pleurodonte* (Simpson, 1895; Kimball, 1947). Various other land snail species have been mentioned as having been collected from the Bowden Beds ("*Thysanophora*", *Opeas striata*, *Succinea lator*; Simpson, 1895; "*Stenogyra*", "*Melaniella*", "*Truncatella*"; Woodring, 1928), but because of the fresh appearance of some of these shells, it has been suggested (Woodring, 1928) that these may be recent material washed into the Bowden

sediments. The Bowden Beds are considered to be of early Pliocene age based on analysis of the foraminiferal fauna (assigned to the *Globorotalia margaritae* zone by Bolli and Bermudez (1965), which was placed in the early Pliocene by Bolli and Premoli Silva (1973)). Recent work on marine mollusks from Bowden has accepted this age assignment (Jung, 1989).

Examination of the collections at the Academy of Natural Sciences of Philadelphia (ANSP) has turned up a new species of land snail collected from the Bowden Beds and belonging to the family Helminthoglyptidae (= Xanthonyceidae *sensu* Eaker (1943) and Nordsieck (1987); = Fruticicolidae *sensu* Turner (1958)). This new species is described below and its relationships are discussed.

Hemitrochus bowdenensis new species

Description: Shell of average size for the genus (*ca.* 11–12 mm diameter), low-trochoidal (height $\frac{2}{3}$ of diameter), moderately thin; spire weakly convex; shell periphery subangular, becoming nearly rounded at the lip; suture deeply impressed; base weakly convex, with the apex of the convexity shifting from a position in the middle of the base in the younger part of the shell to a position nearer to the umbilicus (than to the periphery) as the adult lip is approached; descent of the suture behind the lip unknown, since the upper part of the lip is not preserved in the specimens; lip unreflected at periphery but gradually becomes reflected on the base in the direction of the umbilicus; bordering the umbilicus, the lip is strongly reflected, but only for a short distance, whereas in the middle of the base of the shell, the lip reflection starts earlier but is weaker; the basal insertion of the lip is drawn out, forming a rim on one side of the umbilicus which is reflected over a small part of the umbilicus; aperture round to weakly elliptical, with the width usually slightly exceeding the height; protoconch 1.6–1.7 whorls, smooth; the sculpture of later whorls consists of

¹ Contribution No. 24, Department of Environmental Sciences and Energy Research, Weizmann Institute of Science.

Table 1. Measurements of the type material of *Hemitrochus bowdenensis*.

Specimen	Life history stage	Diameter (mm)	Height (mm)	Height/diameter	Whorl number	Aperture width (mm)	Aperture height (mm)	Aperture height/width
Holotype	adult	12.4 ¹	8.3	0.67	4.5	5.2 ²	4.9 ²	0.94 ²
Paratype	subadult	10.5 ¹	6.9	0.66	4.4	4.6	4.6	1.00
Paratype	?juvenile	8.6	5.5	0.64	4.0	3.9	3.8	0.97

¹ Diameter is the approximate adult diameter; a precise measurement is not possible since the lip is broken.

² Measured 0.1 whorl behind aperture, due to broken lip.

low, broad ribs (ca. 12–14 on the penultimate ¼ whorl) that are parallel to the growth lines and irregular, with each rib varying in both height and width along its length; the length of the ribs also varies, with some disappearing on the dorsum of the shell, and others continuing across the periphery and terminating just below the periphery; on the rest of base, sculpture consists only of irregular growth lines, which get stronger nearer the lip; color opaque white. Measurements of specimens are presented in Table 1.

Material examined: The holotype (ANSP 75798) and two paratypes (ANSP 75799) are the only known specimens of this species. The holotype (figures 1–3) is an adult shell missing the upper lip and the end of the lip where it becomes the umbilical wall. The first paratype (figures 4, 5) is apparently a subadult specimen. The lip shows the reflection which characterizes the adult form but the lip is a little thinner than that of the holotype, suggesting that the shell is not fully mature. The dimensions of the shell should be representative of the adult dimensions, since further growth would result only in thickening of the shell. The upper lip of this specimen is broken as in the holotype but the umbilical end of the lip is intact. The second paratype has the last ca. 1 whorl missing, the remains of which can be seen only as a rim around the umbilicus. An additional ca. ¼ of the upper part of the last whorl was originally present but was removed for amino acid analysis.

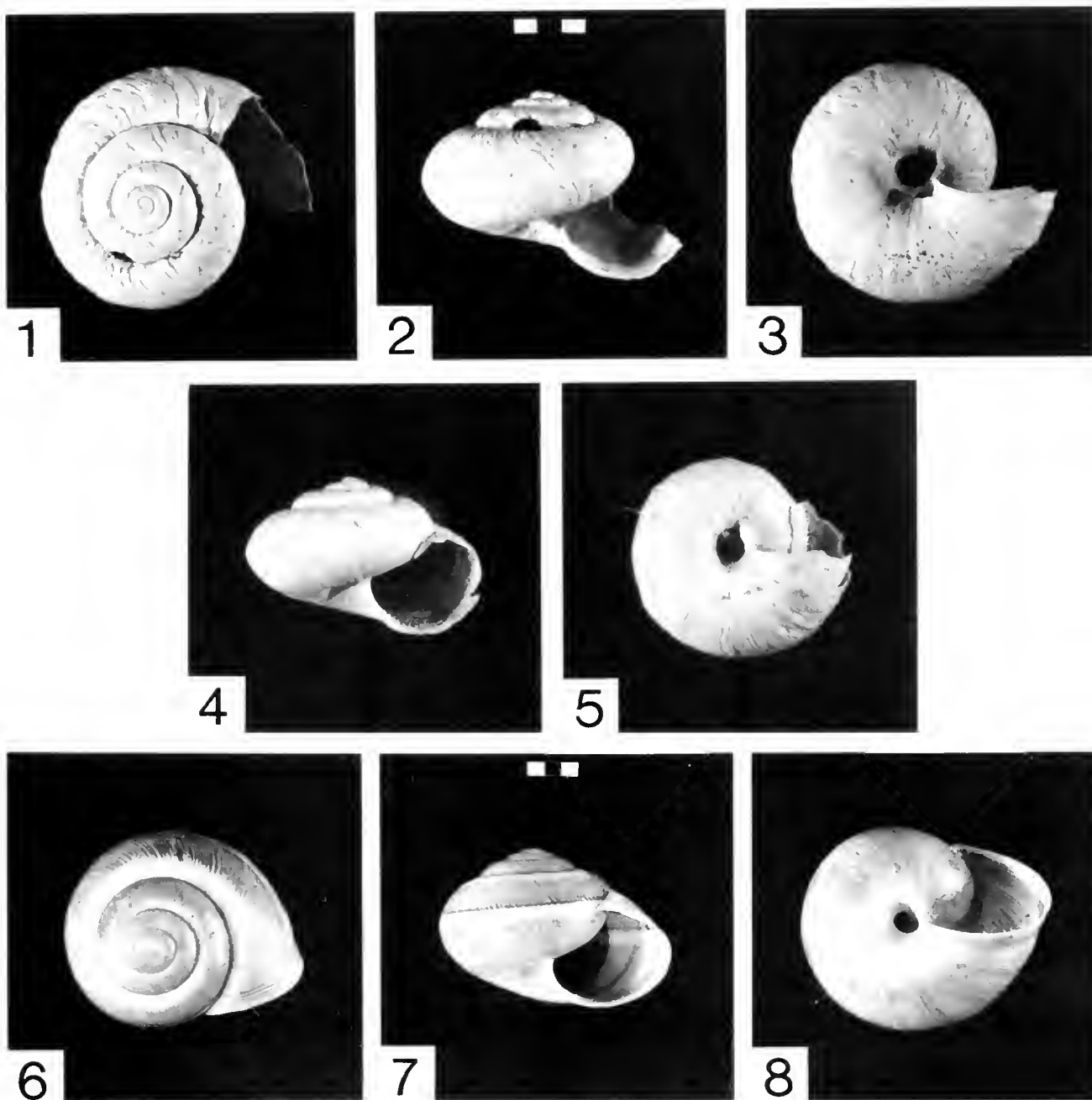
Type locality, stratigraphy, and collection information: The locality data provided with the material indicates that it was collected "Among oligocene fossils, Bowden, Jamaica", by Uselma C. Smith and S. L. Schumo. Bowden is a small village located on the east side of Port Morant Bay in southeastern St. Thomas Parish, Jamaica. No stratigraphic information is provided with the material. However, concerning the well-known Bowden fossil beds (later considered to be Miocene in age; Woodring, 1928), Woodring (1925:7) stated that "At the type locality [i.e., at Bowden] a bed of imperfectly consolidated gravel consisting of small pebbles and grains of igneous rocks, limestone, and other sorts of rock in a marly matrix crops out in the road-cut for a distance of several hundred feet along the bay. This bed, which is not more than 2 or 3 feet thick, contains perfectly preserved fossils, and, so far as known, has furnished all the fossils collected at Bowden." Chubb (1958:28) indicates that at Bowden

there is "one bed, some 2–3 feet thick lying a few feet above road-level, of unconsolidated gravel consisting of small pebbles and grains of igneous rocks in a marly matrix. The bed is lenticular and runs for only about a couple of hundred yards, and it is extremely rich in well-preserved fossils. . . ." The land snail material was among an extensive collection of marine mollusks made by Smith and Schumo and it seems almost certain that all this material was collected from the locality described by Woodring and by Chubb. In a visit to Bowden by the author in April, 1991, it was found that the beds containing marine mollusks run along the roadcut on the east side of the Bowden road, northward from the junction of the road climbing up the hill from Bowden. This should be taken as the type locality for *Hemitrochus bowdenensis*.

No date of collection is associated with the Schumo and Smith collection from Bowden, but the catalogue at the Academy of Natural Sciences of Philadelphia indicates that this material was presented to the museum on January 7, 1902 (G. Rosenberg, personal communication), so it was collected some time before this date.

Comparative remarks: The only other helminthoglyptid genus found in Jamaica is *Dialeuca*. The shells in this genus differ from *Hemitrochus* shells in several respects. The umbilicus (covered in adults) is very narrow and the basal lip inserts at a high angle to the columella (in *Hemitrochus* this insertion is at a low, near vertical angle); these features, together with a higher expansion rate of the last whorl, result in the aperture being considerably wider than high. The basal lip expands gradually and evenly across the base (this also occurs in some Bahamian *Hemitrochus* species) and the dorsal lip is reflected. The sculpture consists only of weak growth lines (this occurs also in some Bahamian *Hemitrochus* species). The ribbed sculpture characteristic of most species of *Hemitrochus* occurs also in *Plagioptycha*, a genus found in Hispaniola, the Bahamas, and the Lesser Antilles. But *Plagioptycha* differs from *Hemitrochus* in having a high-angle insertion of the basal lip onto the columella (as in *Dialeuca*) associated with a relatively wide aperture; the shell is more depressed and a ridge is usually present on the inside of the lower lip on the left (umbilical) side. Thus the new species clearly belongs in *Hemitrochus* rather than in a related helminthoglyptid genus.

Hemitrochus bowdenensis most closely resembles the only other *Hemitrochus* species inhabiting Jamaica, *H.*



Figures 1-3. *Hemitrochus bowdenensis* new species, dorsal, apertural, and ventral views of holotype. 4, 5. *Hemitrochus bowdenensis* new species, apertural and ventral views of paratype 6-8. *Hemitrochus graminicola* (from Happy News, SE of Alexandria, St. Ann, Jamaica), dorsal, apertural, and ventral views. Scale line (in mm) in figure 2 refers to figures 1-5 and scale line in figure 7 refers to figures 6-8.

graminicola (C. B. Adams). *H. graminicola* (figures 6-8) differs in having a more weakly developed sculpture consisting of fine, regular ribs (ca. 30 on the penultimate $\frac{1}{4}$ whorl) which cross the base of the shell, disappearing only near the umbilicus. It also differs in having a rounded periphery on the whole of the last whorl, a more inflated base, less impressed sutures, and a generally larger size (12-16 mm diameter). However, in the form of the lip reflection and in the shift of the apex of the basal

convexity toward the umbilicus in the direction of the lip, *H. bowdenensis* resembles *H. graminicola* precisely. *H. pseudogyra* (Torre) from Cuba closely resembles *H. graminicola* but is less close to *H. bowdenensis* in that its sculpture is both weaker and finer than that of *H. graminicola*. It should be emphasized that, although these are the species nearest phenotypically to *H. bowdenensis*, they are not very closely related to it—the character of the sculpture of *H. bowdenensis* is altogether different

Table 2. D/L amino acid ratios in paratype specimen of *Hemitrochus bowdenensis*.

Amino acid	D/L
Alanine	0.12
Alloisoleucine/isoleucine	0.053
Proline	0.33
Aspartic acid	0.27
Methionine	0.24
Glutamic acid	0.062
Phenylalanine	0.14

from that of any modern species. *H. bowdenensis* is not banded as other *Hemitrochus* species are. The lack of banding on the shells could possibly be the result of fading, but this seems unlikely for such young material.

Hemitrochus has been considered a subgenus of *Cepolis* (Pilsbry, 1939; Baker, 1943), but Turner (1958) raised it to generic status on the basis of anatomical characteristics. Although the earlier inclusion of *Hemitrochus* within *Cepolis* was retained by Nordsieck (1987) and Vaught (1989), the taxonomy of Turner (1958) is followed here.

AGE OF THE SAMPLE

Although the Bowden Beds are considered to be of early Pliocene age, the possibility of inclusion of some modern material in the collections still exists, for example if material were collected from slumped sediments which could have incorporated modern terrestrial shells or from exposed fissure infills. Woodring (1928) considered that some of the land snail material that had been collected from the Bowden Beds may have been modern, stating that some of the material may represent "the remains of living snails that fell into openings in the ground and thus were collected with the fossil material" (p. 109). Because of this possibility, amino acid enantiomer/epimer analyses were carried out on a fragment of one of the *H. bowdenensis* shells as a check on its age (see Goodfriend, 1991, for analytical methods). Material of early Pliocene age would be expected to give D/L amino acid ratios near equilibrium (1.3 for D-alloisoleucine/L-isoleucine and 1.0 for other D/L amino acid ratios) and may be highly depleted in amino acid content.

The analytical results (Table 2) indicate that the *Hemitrochus* shell is relatively young. As would be expected, faster-racemizing amino acids such as aspartic acid, proline, methionine, and phenylalanine (Goodfriend, 1991) show higher D/L ratios than the slower racemizing/epimerizing amino acids glutamic acid and isoleucine. A calibration of the rate of isoleucine epimerization in *Pleurodonte* during the Holocene at a site on the north coast of Jamaica (Goodfriend and Mitterer, 1988) leads to an age estimate based on the alloisoleucine/isoleucine (A/I) ratio of the *Hemitrochus* of 1700 year B.P. (assuming an initial A/I value of 0.013, as is typical of modern land snail shells). This estimate is very approx-

imate since there are a number of errors involved which compound to produce the total error: the error of measurement of the A/I ratio of the *Hemitrochus* sample (5–10%), possible differences in the epimerization rate between different genera (usually on the order of 10%), and, most importantly, the uncertainty of the rate difference between Bowden and the north coast calibration site. For example, a 2° difference between the sites would lead to a 40% difference in the epimerization rates (equation 3 in Goodfriend and Mitterer, 1988). Allowing a total uncertainty of $\pm 50\%$ would indicate a probable age between 800–2400 year B.P. Thus it is clear that the sample is of late Holocene age, and therefore represents material which does not belong to the Bowden Beds. A visit to the Bowden Bed type locality revealed that the mollusk-containing unit was in many cases covered by colluvial material, slumped down from the steep slope above. It seems likely that the *H. bowdenensis* material was collected from such a slumped deposit, perhaps at the same level as the mollusk beds.

DISCUSSION

This new species of *Hemitrochus* is not represented in modern collections from Jamaica and is therefore presumably extinct. Whether this presumed extinction was the result of forest clearance subsequent to European settlement of Jamaica or occurred before this time, as a result of natural processes such as climatic change, cannot be ascertained without additional dated records of this species. Evidence of human induced local extirpations of land snail species exists for the north coast of Jamaica (Goodfriend and Mitterer, 1988). But climatic changes in the late Holocene have also been documented in Jamaica (Goodfriend, 1987).

The occurrence of this apparently extinct species in the recent fossil record of Jamaica is somewhat surprising in view of the fact that other Holocene and late Pleistocene deposits on the island contain only extant species (Goodfriend and Mitterer, 1988; Goodfriend, 1989). Recent extirpations of species in north-central Jamaica (Goodfriend, 1987) and the central north coast of Jamaica (Goodfriend and Mitterer, 1988) have been noted, but these species have survived elsewhere on the island. Local endemics, as *Hemitrochus bowdenensis* may have been, will be more sensitive to environmental changes; when more widespread species undergo local extirpations, local endemics may undergo extinction. The forests of southeastern St. Thomas have been almost completely cut down and replaced by agriculture—degraded forest remains in only a very few areas. One wonders whether other extinct species may turn up in the recent fossil record in this area and other areas that have been similarly degraded.

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Dreissena polymorpha (Zebra Mussel): Colonization of Soft Substrata and Some Effects on Unionid Bivalves

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ABSTRACT

Zebra mussel (*Dreissena polymorpha*) and native bivalve (Unionidae) densities were determined at three sites in southern Lake St. Clair (Ontario) using SCUBA. Lake St. Clair bottom in this area is mostly soft (silty clay) and unionids were virtually the only hard surfaces present. *Dreissena* abundance and biomass increased from west to east: 152 individuals/m² and 26.1 g/m² live mass (west site), to 11,655/m² and 845.8 g/m² (east site). Density of live unionids showed a reverse trend: 2.3/m² and 129.5 g/m² (west site), to 0.1/m² and 16.6 g/m² (east site). At the central and east sites all that was visible of any unionid (live or empty shell) was a mound of *Dreissena*. In a few of those samples, recruitment was so intense that the colony had grown laterally from the original settled surface, resulting in a loose mat of *Dreissena* over the bottom. Among the three sites there was a strong negative correlation between *Dreissena* biomass and abundance of live unionids ($r = -1.0$, $P < 0.01$, $N = 3$). Most of the more heavily colonized unionids showed damage to the posterior valve edges. These data demonstrate that the zebra mussel can not only colonize lakes consisting almost entirely of soft substrata but can reach densities of 10–20 thousand/m² partially by lateral extension of colonies from an original “seed” surface. At such densities they will have a major impact on the benthos, especially indigenous unionid bivalves, which are likely to face virtual elimination.

Key words: *Dreissena polymorpha*, unionids, soft substrata, Lake St. Clair.

INTRODUCTION

Lake St. Clair is part of the Great Lakes drainage system between Lake Huron and Lake Erie. It is a relatively shallow lake, with a mean depth of 3.0m, a length of 43km, and a width of 40km (Leach, 1991). Most authorities believe that the zebra mussel (*Dreissena polymorpha* Pallas, 1771) was first introduced into North America in Lake St. Clair in 1985 or 1986 (Hebert *et al.* 1989, 1991; Mackie, 1991). Since then, it has spread rapidly and is now found in all five of the Great Lakes. Reasons for its remarkable success include relatively high fecundity (ca. 10⁶ eggs/female spawning event; Sprung,

1991), rapid dispersal by passive means either involving drift by veliger larvae or boat/ship dispersal, growth to sexual maturity in one season, and others (Mackie, 1991). In addition, it is ecologically unique, i.e. it has a niche which is not represented in North American fresh waters. Specifically, there is no other attached macrofouling invertebrate of any ecological significance in the Great Lakes. In some areas such as Lakes St. Clair and Erie, relatively high primary productivity and otherwise optimal trophic conditions have further contributed to its success. Information on the distribution and abundance of *Dreissena* in Lake St. Clair has been reported by Hebert *et al.*, 1991, and its biology reviewed by Mackie, 1991. Hebert *et al.* (1989) and Hunter and Bailey (1991) made the observation that *Dreissena* settled on and attached readily to a variety of hard surfaces including the shells of native clams (Bivalvia: Unionidae), of which there are at least 18 species in Lake St. Clair (Nalepa and Gauvin, 1988). Since settled individuals attach by means of a byssus, they require a hard substratum, hence it is often assumed that a soft-bottom lake or river will not support significant zebra mussel colonization.

The purpose of this study was to document the success of *Dreissena* in colonizing one region of a soft-bottom lake, Lake St. Clair, and to provide preliminary evidence of its impact on the community of unionids in that area.

MATERIALS AND METHODS

Three sites in southern Lake St. Clair were sampled for zebra mussels and unionids on 29 and 30 September, 1990 (Fig. 1). All three sites were located on 42°22'3" N latitude which is roughly parallel to and about 5 miles north of the southern shoreline of Lake St. Clair in Canadian waters (Ontario). The site farthest west (henceforth the “west site”) was at 82°47'30" W; the central and east sites were at 82°40'00" W and 82°32'30" W, respectively. Total distance between adjacent sites was about 10.3 km (6.4 mi; Fig. 1). These sites were the same as locations 15, 18, and 21 of Pugsley *et al.*, 1985, and

two of them, the west and east sites, were also sampled by Nalepa and Gauvin (1988). The depth at each site was 6.0 ± 0.61 m.

The bottom of Lake St. Clair is nearly all soft sediment, the main component of which is muddy sand, especially in the central part, with areas of gravel sand closer to shore (Leach, 1991). In the areas sampled here, the surficial sediment was virtually the same from site to site; silty clay overlain by a thin layer of detritus. The lake bed was relatively flat with few low undulations. Macrophytes were almost non-existent and nearly the only visible solid substrata consisted of mounds of zebra mussels.

Zebra mussel and unionid sampling were done using SCUBA in two dive teams working independently, with two members per team. An aluminum square frame of 0.25 m^2 area was used to obtain a series of samples by casting (throwing forward) the frame, then by touch, collecting all hard objects to a depth of approximately 2 cm into the sediment. All objects within each quarter m^2 were separately bagged, brought to the surface, labeled, and returned to the laboratory for further analysis. Sampling was not statistically random, however due to the poor visibility (30–50 cm), bottom features, including mounds of zebra mussels, were not visible to the divers when the quarter m^2 frames were cast. Therefore this procedure was relatively free of sampler bias. Each dive team moved about 1–2 m further over the bottom between successive samples. Sampling protocol required that a total of ten "hits" were needed for each dive team in order to finish a site. A hit was a sample containing at least one zebra mussel. Underwater records were kept of total casts so that misses could later be used for density calculations. Hence the data reported here are based on a different number of casts (=samples) at each site, with each site having 20 hits.

In the laboratory, each quarter m^2 sample was individually examined. All hard surfaces (mostly unionid shells) were scraped free of zebra mussels by cutting the byssal threads. Removed mussels were rinsed free of sediment and the rinse water collected and passed through a 0.5 mm sieve in order to recover small individuals. The smallest zebra mussels, mostly 0.2–0.5 mm shell width, were not retained by this process, because the large volumes of animals and sediment made working with smaller meshes impractical. Care was taken to separately record clusters of zebra mussels that were not attached to any other hard surface. After draining, the zebra mussels from each quarter m^2 sample were pooled for weighing. Live unionids were also cleaned, weighed, and prepared for identification. All weights reported herein are total (shell + soft tissues) live weight. A random subsample of zebra mussels from each site was preserved in 10% formalin (neutralized with CaCO_3) and used for shell length measurements. Length measurements were to the nearest 0.1 mm. From these data, density vs. size class plots could be done by site.

Dreissena shell to tissue mass was determined by drying to a constant mass at 70°C , animals that had been

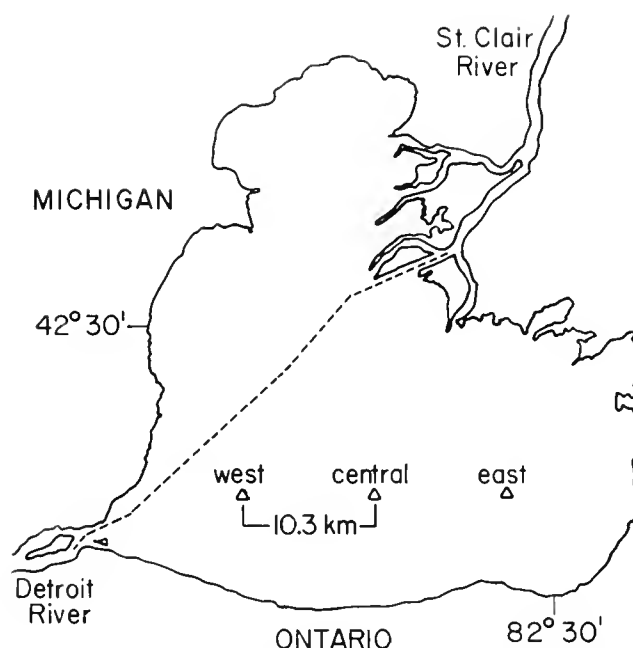


Figure 1. Location of the three sample sites in Lake St. Clair. The shipping channel is shown as a dashed line.

sorted by shell length. Whole dry animals were decalcified using 5% HCl for 2 hours or until CO_2 evolution stopped. This method gives identical results to "ashing" methods (Hunter and Lull, 1976). The remaining non-shell material (internal tissues + periostracum) was dried and weighed giving "tissue" dry mass. Computed from these values was the shell:tissue mass ratio which is simply shell mass divided by tissue mass, a number which is a useful index of the general condition of the animal.

RESULTS

A total of 104 quarter m^2 samples were taken. At the west site, out of 43 quarter m^2 samples (=casts), 20 had *Dreissena* (=hits) and 23 did not (=misses), i.e., 53.5% of the 43 casts contained no zebra mussels. Numbers for the other two sites were: 33 casts, 13 misses for the central site (39.4%); and 28 casts, 8 misses for the east site (28.6%). Table 1 gives the abundance and biomass for *Dreissena* and for unionids at the three sites. *Dreissena* density was greatest at the east site averaging 11,655 individuals/ m^2 and 845.8 g/ m^2 ; and lowest at the west site, averaging 152 individuals/ m^2 and 26.1 g/ m^2 . Each of the sites differed significantly in biomass from the other two (one-factor ANOVA, $P=0.0001$; Scheffe's F-test, $P<0.01$). In terms of abundance, the west and central sites were not significantly different but the other comparisons (west and east; central and east) were significantly different (one-factor ANOVA, $P<0.0001$; Scheffe's F-test, $P<0.01$). Both biomass and abundance increased from west to central to east site. The maximum biomass of *Dreissena* recorded for any sample was at the east site at 1409 g/ m^2 which corresponds to 19,417 individuals/ m^2 .

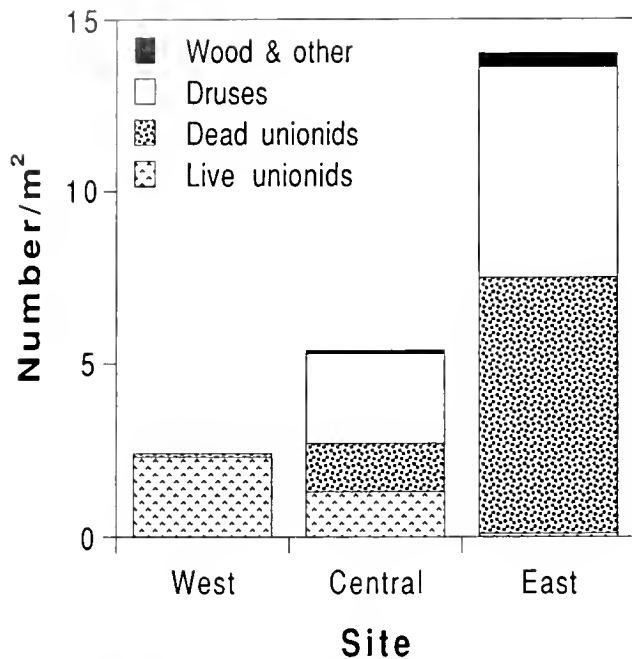


Figure 2. Mean density of hard substrata in Lake St. Clair by type of material and by site. Druses are discrete clusters of zebra mussels.

In contrast to *Dreissena* density trends, density of live unionids was highest at the west site and decreased moving to the central and east sites (Table 1). Unionid density was greatest at the west site averaging 2.3 individuals/m² and 129.5 g/m². Out of 28 quarter m² samples at the east site, only one live unionid was found. At the west site there were 24 live individuals found over 43 quarter m² samples. The data for the east site were non-normal due to the presence of zeros for all but one sample. For purposes of statistical analysis, a small number (0.01) was added to all values which were then log (ln) transformed. This transformed data set was then statistically analyzed for differences between sites. For both biomass and abundance, there were significant differences among sites (one-factor ANOVA, $P < 0.002$), and the east site differed significantly from the other two (Scheffe's F-test, $P < 0.01$).

It was readily apparent by inspection of the lake bottom earlier in the season, when visibility was 2.5–3.5 m,

that hard substrata in this general area of the lake consisted of small, discrete objects imbedded in the soft bottom. Later observations indicated they were fairly common, ranging from about 2.4 objects/m² at the west site to 14 objects/m² at the east site, and they were sufficiently small so as not to cover a very large proportion of a square meter except in a few of the east samples. With the exception of 3 pieces of wood, and two snail shells (*Elimia livescens* Menke 1830), all of these hard substrata were either unionids, unionid shells, or independent clusters of zebra mussels (Fig. 2). The density of live unionids at the three sites has been presented in Table 1 and is shown in Fig. 2 relative to other hard substrata. The number of dead unionids (shells only with both valves usually connected), shows a reverse trend to that of the living unionids. There was, on average, 0.1 shell at the west site, 1.4 at the central, and 7.4 at the east site. Likewise the number of *Dreissena* clusters (druses) that were independent from other hard substrata also increased from west to east (0 west, 2.6 central, and 6.1 east; Fig. 2).

Figure 3 illustrates the negative correlation between *Dreissena* biomass and unionid abundance. This correlation is significant $P < 0.01$, $r = -1.0$, $N = 3$. The plot of unionid density also shows the ratio of live to dead (L:D) animals by site. At the west site there were 25 live individuals for every dead unionid. This ratio was 0.9:1 at the central site, whereas at the east site there was only a single live unionid, giving an L:D ratio of 0.02:1.

Based on subsamples of fixed material, size distributions of *Dreissena* were expressed on a per m² basis (Fig. 4). It is evident that at both the central and east sites there was substantial recent recruitment based on the large group of juveniles from about 1 to 5 mm shell length. Fifty-two percent of the central sample and 62% of the east sample were made up of juveniles 5 mm or less.

In contrast, at the west site there was a pronounced absence of *Dreissena* in these smaller juvenile size classes (Fig. 4). The smallest animal in the west subsample was 2.6 mm and only 3% of the subsample was less than 5 mm shell length. Larger size classes were well-represented especially in the central and east subsamples. For example at the central site, 34% of the subsample was comprised of mussels measuring 12 mm or greater, com-

Table 1. Mean abundance and biomass (\pm SE) for *Dreissena* and for unionids at three sites in southern Lake St. Clair. Only a single live unionid was found in the east samples.

	Site in Lake St. Clair		
	West	Central	East
<i>Dreissena</i> density			
Number/m ²	152 \pm 36.9	2,847 \pm 620.9	11,655 \pm 2,000.4
Biomass (g/m ²)	26.1 \pm 6.34	402.1 \pm 87.69	845.8 \pm 145.17
Unionid density			
Number/m ²	2.3 \pm 0.49	1.3 \pm 0.25	0.1
Biomass (g/m ²)	129.5 \pm 27.79	73.4 \pm 14.69	16.6

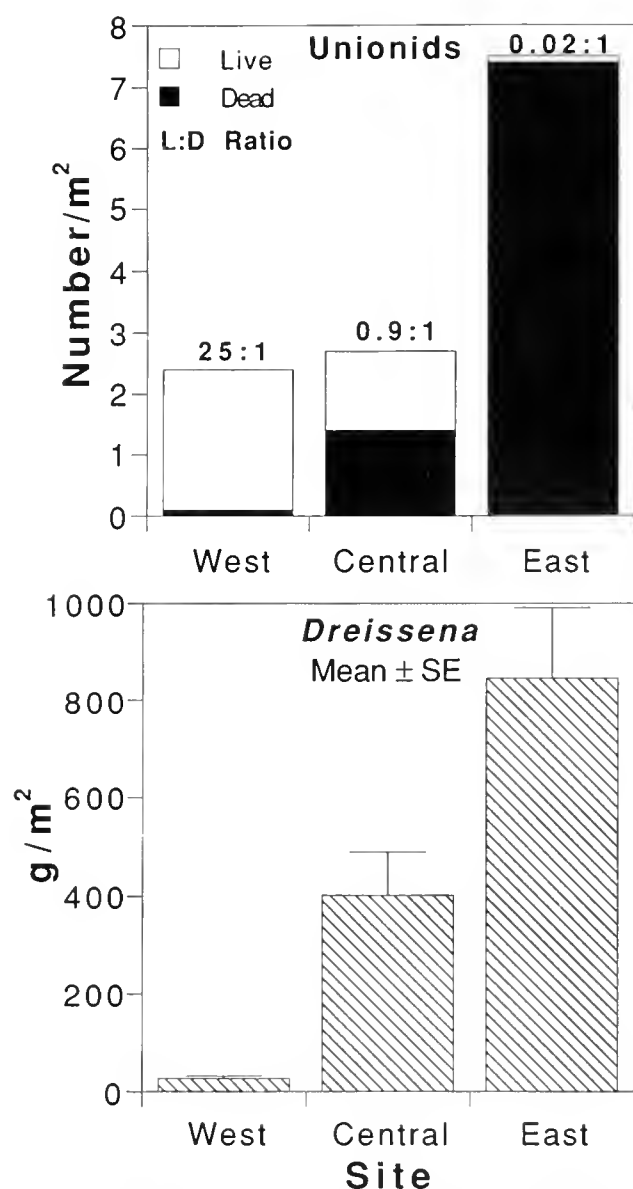


Figure 3. Mean abundance of live and dead (empty shells) unionids by site (upper plot) and mean biomass of *Dreissena* (lower plot) by site in Lake St. Clair.

pared to 12% at the east and 9% at the west sites. Although ages were not determined from this material, it is likely that the majority of *Dreissena* measuring 12 or more mm were at least one-year-old.

In addition to the above differences, the condition of the animals differed among the sites. There was a tendency for the central and especially the east animals to have areas of eroded shell, i.e. patches where the periostracum was clearly missing revealing the underlying whitish CaCO₃. Although no data were recorded, there was also a higher proportion of empty *Dreissena* shells at the east site suggesting that mortality rates were substantially higher there. Not only were west site densities far lower (there were major areas of live unionid shell

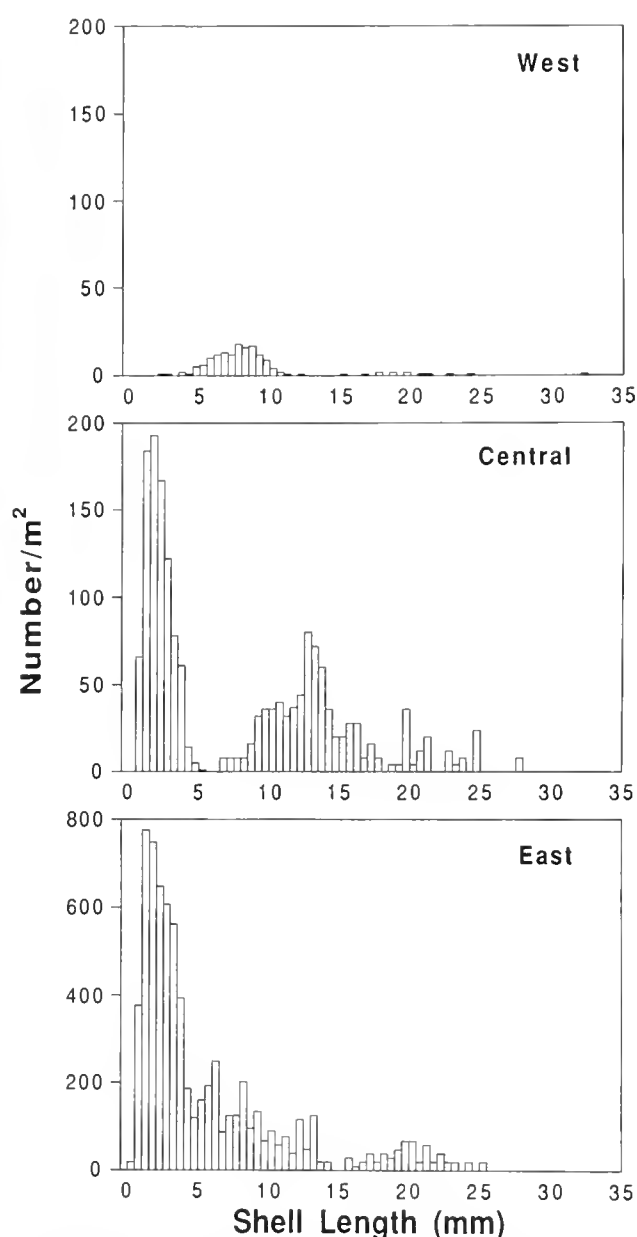


Figure 4. Density of *Dreissena* by shell length size class at three sites in Lake St. Clair.

surface unoccupied by zebra mussels) but the *Dreissena* there had shells with fully intact periostraca.

Figure 5 shows the relationship between shell length and shell:tissue mass ratio for each site. The general tendency is that as the mussels grow (increase in length) their shell:tissue ratio also increases, with a fairly linear relationship between the variables. Smaller size animals (<10 mm shell length) do not differ much between sites and their shell:tissue ratios are mostly within the range of 7–10. In contrast, larger animals (>20 mm) show widely differing shell:tissue ratios at different sites (Fig. 5). For example, a 25 mm animal from the east site would have a dry tissue mass averaging 34 mg and a dry shell

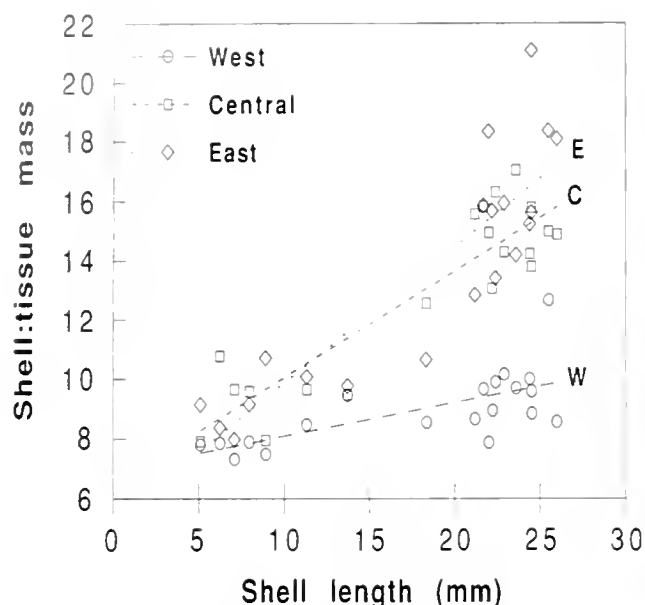


Figure 5. Shell to tissue mass ratio vs shell length for *Dreissena* at three sites in Lake St. Clair.

mass of 552 mg giving a shell:tissue ratio of 16.2. Animals at the central and west sites of the same 25 mm length would have 54 and 86 mg dry tissue and 812 and 821 mg dry shell for a shell:tissue ratio of 15.0 and 9.5 respectively. When groups of mussels over 20 mm shell length were compared across the three sites, the east and central sites were not significantly different in shell:tissues mass ratio, however the west site differed from the other two (one-factor ANOVA, $P < 0.0001$; Scheffé's F-test, $P < 0.01$). In other words, larger sized *Dreissena* at the east and central sites are "tissue-deficient" compared to west site animals.

It was evident from close inspection of the unionid shells whether of live or dead material, that many of them showed damage to their posterior valve edges which was a direct result of dense aggregations of *Dreissena*. An *Anodonta grandis* that is heavily infested with zebra mussels is shown in Fig. 6. The posterior one third to one half of this and other species is typically covered with a thick and solid mass of *Dreissena*, often more than 2 cm thick. *Dreissena* attachment of this magnitude renders normal valve movement virtually impossible and activities normally occurring through the gape (feeding, reproduction, respiration, locomotion, etc.) are severely curtailed. The resulting damage, illustrated in Figs. 7 and 8 with *Lampsilis siliquoidea*, involved substantial deformation of the shell so that the normally gradual curve of the posterior valve border was jagged or indented. The majority of specimens collected had levels of damage that fell between the extremes shown in Figs. 7 and 8. In some specimens, this damage extended internally so that the nacre was rough, irregular, and or discolored. In a few individuals the damage was so extensive that a gap of 2–5 mm remained at the posterior edge even through the valves were fully closed (Figs. 7 and 8). For



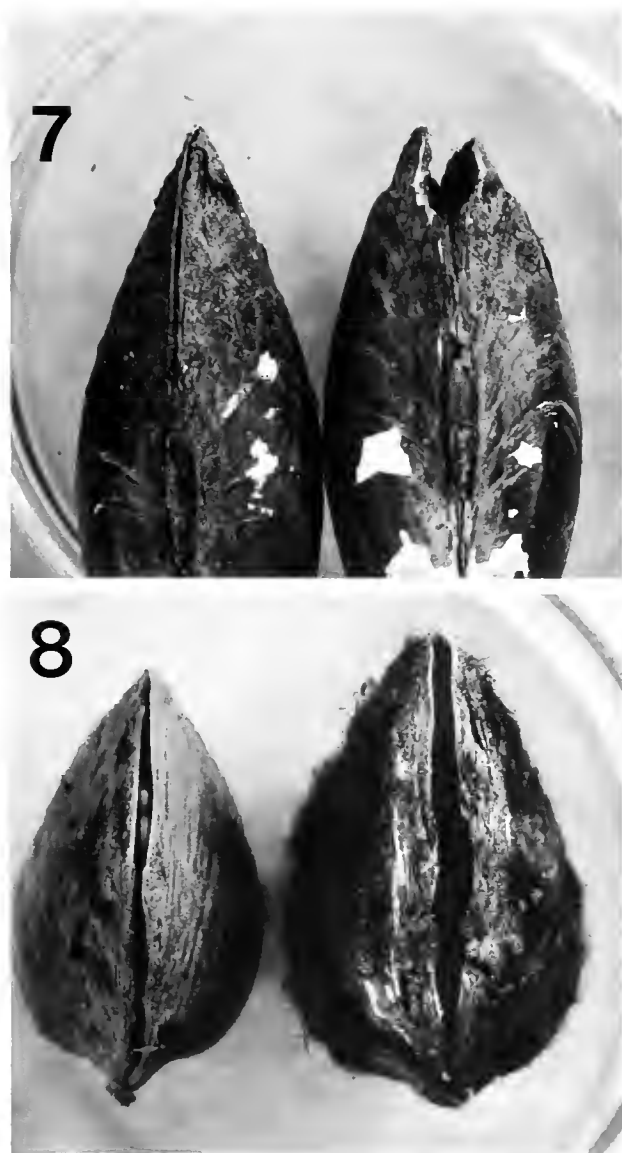
Figure 6. Specimen of *Anodonta grandis* from Lake St. Clair that has been heavily colonized by *Dreissena polymorpha*. Such colonized individuals ranged from about 5.5–9.5 cm in length. *Anodonta* is shown posterior end up.

Lampsilis siliquoidea, the only species for which there was sufficient material, 22.5% of the shells had no damage, 55% had moderate damage, and 22.5% had relatively heavy damage.

Nine species of unionids were found among the three sites (Table 2). For six of the species, at least one live individual was obtained, but three species, *Lampsilis ventricosa*, *Truncilla truncata*, and *Elliptio dilatata*, were represented only by empty shells. The unionid fauna from these sites was dominated by *Lampsilis siliquoidea*, such that this species comprised 79.4% of all the live unionids collected. When empty shells alone are considered, then *L. siliquoidea* comprised 67.8% of the unionid community, suggesting that its dominance has recently increased. For all of the species found, the number of dead individuals was greater than or equal to that of the live individuals.

DISCUSSION

A number of European investigators have reported on unionids as a substratum for *Dreissena*. Sebestyen (1938: 178) concluded that there was "no doubt that *Dreissena* has a decided ill effect on unionidae." In that same study it was observed that the native unionids (6 species) were



Figures 7–8. Dorsal (7.) and posterior (8.) views of two *Lampsis siliquioidea* shells from Lake St. Clair from which all attached *Dreissena* have been removed. The shells on the left are nearly normal, whereas the shells on the right show considerable damage. One (8.) appears fuzzy due to remaining byssal threads. Shells are between 6 and 7 cm in length.

in danger of disappearing entirely from Lake Balaton, Hungary. Sebestyen (1935) suggested that the interaction resulted in interference with locomotion and reduction in food supply for the unionids. In contrast, Lewandowski (1976) concluded that *Dreissena* had no unfavorable effects. In spite of this finding, he cited other European studies that identified the interaction as one of a competitive nature. There was evidence that *Dreissena* caused a slight negative effect on growth in shells of younger individuals and that in older unionids, the shells of *Dreissena*-infested individuals were thicker than shells of *Dreissena*-free individuals. The body (soft-tissue) weight

Table 2. Mean abundance of unionids by species for all three Lake St. Clair sites combined. Dead = empty shells. Total area sampled = 26 m², so that a density of 0.04 m² corresponds to one individual.

	Number/m ²	
	Live	Dead
<i>Lampsilis siliquioidea</i> (Barnes, 1823)	1.04	1.73
<i>Leptodea fragilis</i> (Rafinesque, 1820)	0.12	0.23
<i>Proptera alata</i> (Say, 1817)	0.04	0.15
<i>Anodonta grandis</i> (Say, 1829)	0.04	0.04
<i>Ligumia nasuta</i> (Say, 1817)	0.04	0.04
<i>Fusconaia flava</i> (Rafinesque, 1820)	0.04	0.04
<i>Lampsilis ventricosa</i> (Barnes, 1823)	0	0.23
<i>Truncilla truncata</i> Rafinesque, 1820	0	0.04
<i>Elliptio dilatata</i> Rafinesque, 1820	0	0.04

was not significantly altered by infestation. Lewandowski (1976) also observed posterior shell deformations in some of the *Anodonta piscinalis* and speculated that the siphonal region was particularly attractive to post-veliger *Dreissena*.

It is likely that the intensity of the infestations with which Lewandowski was working, (20 *Dreissena* on each unionid, specifically *Anodonta piscinalis*) was below the level required to cause an observable impact. The above densities are comparable to those reported here for the west site but are much lower than occur in the central or east sites in southern Lake St. Clair.

Hebert *et al.* (1989) observed that *Dreissena* is often located on unionid shells in Lake St. Clair. They considered *Dreissena* to be an "interference competitor" of native mussels (Hebert *et al.*, 1989; 1991). Field experiments in Lake Erie have shown that *Dreissena* has both species and sex-specific effects on unionids (Haag *et al.*, 1991).

Two bits of data presented in this study are strongly suggestive that *Dreissena* is having a negative impact on the community of unionids in those areas of Lake St. Clair where *Dreissena* densities are relatively high. This evidence includes the negative correlation between *Dreissena* biomass and unionid density, as well as damage to unionid shells beneath *Dreissena* accumulations (Hunter and Bailey, 1991). Negative impact of *Dreissena* on unionids was also shown by Hebert *et al.*, (1991) who reported that heavily infested unionids had half the lipid reserves as unaffected individuals. Mackie (1991) concluded that heavy infestations of *Dreissena* cause several kinds of negative effects on unionids, some of which interfere with normal locomotion. Unequivocally demonstrating that zebra mussels cause death of unionids is difficult since direct observation of death is impractical and the cause is likely to be multifactorial. Unionids also die of a variety of other causes resulting in empty shells on which *Dreissena* can settle. Hence, observation of unionid shells colonized by *Dreissena* is not necessarily evidence that they were the cause of death. Observation of empty unionid shells bearing deformation to the posterior valve edges of the sort illustrated in Figs. 7 and 8,

is strongly suggestive that *Dreissena* has played a role in the death since there is little else that will cause this kind of damage (R. Hoeh, pers. comm.).

This study also suggests that the general health or condition of zebra mussels is inversely related to their density. Specifically, where the population density is high, as is the case at the central and east sites, the larger animals are emaciated. The result is a shell to tissue mass ratio that is high compared to that of animals from low density situations, i.e., under such conditions adult-sized shells contain an undersized mass of tissue. As larger (older) individuals are settled on and overgrown by more recent recruits, it is likely they experience increasingly suboptimal conditions, resulting in an emaciated animal. Tissue degrowth under poor trophic conditions is known to occur in gastropods (see Russell-Hunter and Eversole, 1976) and it is likely to be occurring in *Dreissena*-infested unionids as well.

Stanczykowska (1975) concluded that as the *Dreissena* population density increased, their condition decreased. Her findings were based largely on size and weight data, i.e., animals of specific age groups in dense populations (e.g., 700/m²) tended to be smaller in both length and weight than those from low density conditions (e.g., 30/m²).

Size-distribution data suggest that there are certainly two and probably three year-classes present at each site. This contention agrees with other studies which indicate that *Dreissena* in both Lakes Erie and St. Clair can grow to well over 10 mm shell length in one year (Nichols *et al.*, 1991; Mackie, 1991). Thus the largest individuals sampled (i.e., 20 mm shell length) are likely to be in their second year with a few larger individuals possibly three years old. The timing of recruitment of the most recent cohort is distinctly different at the west site compared to the other two (Fig. 4). At the west site there is an absence of small juveniles, whereas they are well represented at both the central and east sites. The modal size for juveniles (defined here as individuals <10 mm shell length) at both the central and east sites was 2 mm. Forty-three percent of the central sample and 35% of the east sample consisted of juveniles less than 3 mm shell length. It would appear that a relatively intense but brief recruitment of post-veligers occurred at the west site perhaps 4–8 weeks before these samples were taken, resulting in a relatively well-defined cohort of about 5–10 mm in late September (as seen in Fig. 4). In contrast, a more recent recruitment is in evidence at the other two sites beginning perhaps four weeks previously and possibly still continuing or just ending as of late September. It appears that there was little recruitment activity at the central site during the time when recruitment was intense at the west site (Fig. 4).

These contrasting recruitment patterns are likely to be due to differences in veliger density in different major water masses and to wind-induced irregularities influencing the extent of these water masses. Water on the western and northwestern side of the lake ("Huron" water) is largely from the Lake Huron/St. Clair River flow

system (Leach, 1980, 1991). Huron water is relatively veliger-poor due to very low *Dreissena* density in that area in 1990, which would result in low recruitment around the west site. Water in eastern and southeastern Lake St. Clair ("St. Clair" water) is more stable and productive due to nutrient enrichment from Ontario rivers (Leach, 1980, 1991). In this water mass *Dreissena* reached much higher densities (eg. central and east sites) than elsewhere in the lake. Changing wind speed and direction move the boundaries of these water masses to some degree. If the St. Clair water mass extended over the west site for a few days in summer, then it could produce the recruitment pulse that is seen in September as a distinct cohort of settled juveniles.

Two of the sites sampled in this study (west and east) were approximately the same as sampled by Nalepa and Gauvin (1988) in their study of unionid distribution in Lake St. Clair. Since their samples were taken in September, 1986, they contained no zebra mussels. The average unionid density they reported for the southern half of Lake St. Clair was $2.6 \pm 1.91/\text{m}^2$ ($\bar{x} \pm s$, N=15) compared to the average for the present study of $1.2 \pm 1.10/\text{m}^2$ (N=3). Nalepa and Gauvin (1988) found 18 species of unionids of which nine were the same as those in Table 2. Of the nine species listed in Table 2, four were represented by empty shells only. Although they collected material from a much larger area it is interesting to note that seven out of nine species common to the two studies, declined as a percentage of the total numbers collected. Only *Lampsilis siliquoidea* (= *L. radiata siliquoidea* of Nalepa and Gauvin, 1988) increased substantially as a proportion of the total unionid community. That species comprised 45% of Nalepa and Gauvin's unionid abundance whereas it was 79% of our samples. Although the goals of these two studies differ, it is possible that *L. siliquoidea* may be less affected by *Dreissena* colonization than other species hence has become an even more dominant member of the unionid community than it was before. In their study, Nalepa and Gauvin concluded that the diversity and composition of unionids in Lake St. Clair appeared to be relatively unchanged since the turn of the century. With the introduction of the zebra mussel at very nearly the same time and location as their study, the unionid community will now undoubtedly change very substantially. Because no indigenous species appears to be able to tolerate or escape *Dreissena* colonization, it is likely that the unionid community in Lake St. Clair will be virtually eliminated in a few year's time.

ACKNOWLEDGEMENTS

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water masses. Special thanks are due to LCDR Luke Clyburn (NSCC) for providing the boat transportation and dive support. Randy Hoeh (Univ. of Michigan, Museum of Zoology) kindly identified or confirmed our identification of the unionids.

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New Ecphoras (Gastropoda: Thaididae: Ecphorinae) from the Calvert Formation of Maryland (Langhian Miocene)

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ABSTRACT

Three new ecphoras are described from the relatively unstudied Shattuck Zones 12 and 14 of the Plum Point Member of the Calvert Formation (Langhian Miocene) of Maryland. The new species, *Ecphora* (*Ecphora*) *chesapeakeensis* n.sp., *Ecphora* (*Ecphora*) *turneri* n.sp., and *Ecphora* (*Trisecephora*) *scientistensis* n.sp., fill in gaps in the evolutionary lineages of the *Ecphora gardnerae* species complex, the *Ecphora choptankensis* species complex, and the *Ecphora* (*Trisecephora*) *tricostata* species complex, respectively.

Key words: *Ecphora*; Gastropoda; Calvert Formation; Miocene; Maryland.

INTRODUCTION

Since the publication of the "Field Guide to the Ecphoras" (Petuch, 1989), three new species of *Ecphora* Conrad, 1843 have been brought to my attention. These were collected in the relatively unstudied Beds 12 and 14 (Zones 12 and 14 of Shattuck, 1904:xxvii) of the Calvert Formation (Plum Point Member), along the Calvert Cliffs of western Chesapeake Bay, in Calvert County, Maryland. As the preservation of the molluscan fossils of Beds 12 and 14 is not good, the result of extensive leaching by groundwater, most specimens of upper Calvert ecphoras are collected in a fragmentary state. In spite of this difficult collecting of extremely fragile and shattered specimens, Mr. Joseph Turner of Baltimore, Maryland, through great diligence and patience, has managed to extract a number of unusual forms from these virtually unworkable beds. Through his generosity in the donation of numerous study specimens, I was able to determine that three ecphoras were new to science, and these are described here. This paper is considered an addendum to "Field Guide to the Ecphoras."

The three new species fill gaps in the evolutionary lineages of three main groups of ecphoras. One new species, here named *Ecphora* (*Ecphora*) *turneri* n.sp., is morphologically intermediate between *E. (Ecphora) wardi* Petuch, 1989 (figure 5) from Bed 10 of the Calvert Formation (Langhian Stage, Miocene) and *E. (Ecphora) choptankensis vokesi* Petuch, 1989 (figure 6) from Bed

16 of the Choptank Formation (Serravallian Stage, Miocene). Likewise, a new three-ribbed ecphora, here named *Ecphora* (*Trisecephora*) *scientistensis* n.sp., is intermediate between *E. (Trisecephora) eccentrica* Petuch, 1989 (figure 9) of Bed 10 of the Calvert Formation and *E. (Trisecephora) smithae* Petuch, 1988 (figure 11) from Bed 16 of the Choptank Formation. The third new species, here named *Ecphora* (*Ecphora*) *chesapeakeensis* n.sp., is the oldest known member of the *E. (Ecphora) gardnerae* Wilson, 1987 species complex. This new ecphora is ancestral to *E. (Ecphora) williamsi* Ward and Gilinsky, 1988 (figure 2) from Bed 19 of the Choptank Formation, which previously had been thought (Petuch, 1989) to have been the original progenitor of the wide-ribbed *E. gardnerae* species group.

In this paper, I use the morphological criteria for ecphora species-level determinations that are outlined in my earlier works (Petuch, 1988, 1989). The holotypes of the new taxa are deposited in the invertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and bear UF numbers.

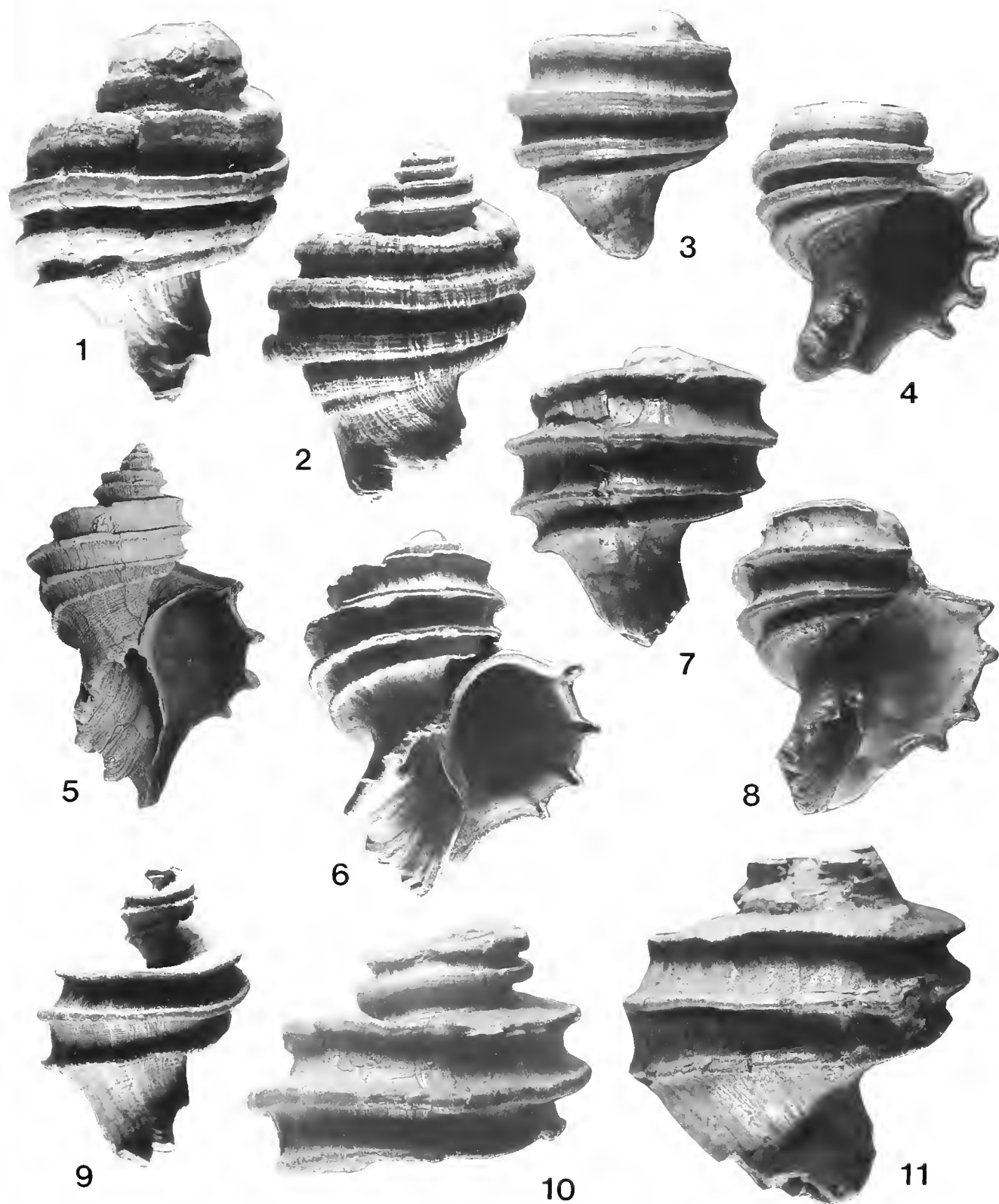
SYSTEMATICS

Class Gastropoda
Subclass Prosobranchia
Order Caenogastropoda
Superfamily Muriceae
Family Thaididae
Subfamily Ecphorinae Petuch, 1988
Genus *Ecphora* Conrad, 1843

Ecphora (*Ecphora*) *chesapeakeensis* new species
(figures 3, 4)

Materials examined: *Holotype:* Length (incomplete and reconstructed) 28 mm, in Shattuck Zone 14, Plum Point Member, Calvert Formation, at Scientists Cliffs, Calvert County, Maryland, Chesapeake Bay, UF 23798; *Paratype:* length (incomplete and reconstructed) 35 mm, same locality as holotype, Petuch collection.

Description: Shell cylindrical in shape, slightly inflated; shoulder rounded; body whorl ornamented with 4 large,



Figures 1–11. *Ecphoras* from the Miocene of Maryland. 1. *Ecphora* (*Ecphora*) *calvertensis* Petuch, 1988, dorsal view of 43 mm specimen, Shattuck Zone 12, Calvert Formation. 2. *Ecphora* (*Ecphora*) *williamsi* Ward and Gilinsky, 1988, dorsal view of 57 mm specimen, Shattuck Zone 19, Choptank Formation. 3. *Ecphora* (*Ecphora*) *chesapeakeensis* n.sp., ventral view of holotype, length (incomplete) 28 mm, UF 23798, Shattuck Zone 14, Calvert Formation. 4. *Ecphora* (*Ecphora*) *chesapeakeensis* n.sp., ventral view of paratype, length (incomplete) 35 mm, Shattuck Zone 14, Calvert Formation. 5. *Ecphora* (*Ecphora*) *wardi* Petuch, 1989, ventral

wide, rounded, adherent cordlike ribs that are slightly "T"-shaped in cross section; ribs sculptured with 1–4 thin, impressed spiral threads; shoulder rib largest and widest, curving upward (posteriorward) to produce cancellate spire whorls; wide shoulder rib slightly incurved, producing distinctly rounded appearance; areas between ribs relatively smooth, with only few very fine spiral threads; siphonal canal well developed, ornamented with numerous large spiral threads; umbilicus narrow.

Etymology: Named for the Chesapeake Bay, which borders the type locality.

Discussion: *Ecphora chesapeakensis* is closest to *E. williamsi* Ward and Gilinsky, 1988 (figure 2) from the younger Choptank Formation, and appears to be its direct ancestor. The new species differs from its Choptank descendant in being a smaller, less inflated shell with thinner, less rounded ribs. The ribs of *E. williamsi* are lower and more adherent, while those of *E. chesapeakensis* project farther from the body whorl. Both species have similar wide, rounded, incurved shoulder ribs. *Ecphora chesapeakensis* is also similar to *E. calvertensis* Petuch, 1988 (figure 1) from Shattuck Zone 12, but differs in having distinctly rounded, cordlike ribs instead of the sharply-flanged, "T"-shaped ribs of the older Calvert species. This new *ecphora* constitutes a morphological link between the generalized *E. calvertensis* and the *E. gardnerae* species complex of the later Miocene. *Ecphora chesapeakensis* is confined to Shattuck Zone 14 (Bed 14, Calvert).

Ecphora (Ecphora) turneri new species
(figures 7, 8)

Material examined: *Holotype:* Length (incomplete) 38 mm, in Shattuck Zone 14, Plum Point Member, Calvert Formation, approximately 1 km north of Governor Run, Calvert Cliffs, Calvert County, Maryland, Chesapeake Bay, UF 21465, *Paratype:* length 41 mm, same locality as holotype, Petuch collection.

Description: Shell cylindrical in shape, with sharply angled shoulder; body whorl ornamented with 4 thin, narrow, blade-like ribs; edge of ribs rounded; subsutural areas flattened, producing stepped, scalariform spire; areas between ribs smooth, without spiral sculpture; siphonal canal elongated, umbilicus narrow but well developed.

Etymology: The taxon honors Mr. Joseph Turner of Baltimore, Maryland, who generously donated a large suite of research material from Shattuck Zones 12 and 14 of the Calvert Formation.

Discussion: *Ecphora turneri* is closest to *E. choptankensis vokesi* Petuch, 1989 (figure 6) from Shattuck Zone 16 of the Choptank Formation, but differs in being a much smaller, much more cylindrical and slender shell, with lower, less projecting ribs. The umbilicus of *E. turneri* is also much narrower than that of *E. choptankensis vokesi*, and the new species has a proportionally longer siphonal canal. *Ecphora turneri* is confined to Shattuck Zone 14 (Bed 14, Calvert).

Subgenus *Triscephora* Petuch, 1988

Ecphora (Triscephora) scientistensis
new species
(figure 10)

Material examined: *Holotype:* Length (incomplete, fragmentary) 29 mm, in Shattuck Zone 12, Plum Point Member, Calvert Formation, at Scientists Cliffs, Calvert County, Maryland, Chesapeake Bay, UF 23799.

Description: Shell cylindrical, slightly inflated in shape; shoulder sharply angled; subsutural area flattened, planar; spire whorls scalariform, stepped; body whorl ornamented with 3 large cordlike ribs; ribs rounded on edges, sculptured with 1 or 2 faint, shallow impressed spiral threads; areas between ribs smooth, without spiral sculpture.

Etymology: Named for the Scientists Cliffs, Calvert County, Maryland, the type locality.

Discussion: *Ecphora (Triscephora) scientistensis* is closest to *E. (Triscephora) eccentrica* Petuch, 1989 (figure 9) from Shattuck Zone 10 of the Calvert Formation, but differs in being a more cylindrical shell, by lacking fine spiral threaded sculpturing between the ribs, and by having a lower, adherent spire that does not become detached and uncoiled. The ribs of *E. (Triscephora) scientistensis* are also thicker than those of *E. (Triscephora) eccentrica*. The new species is also somewhat similar to *E. (Triscephora) tricostata* Martin, 1904, also from Zone 10, but that well known species has wider ribs that are "T"-shaped in cross section and also has a more inflated, globose shell. *Ecphora (Triscephora) tricostata*, like *E. (Triscephora) eccentrica*, has detached, uncoiled whorls, while the whorls of *E. (Triscephora) scientistensis*

view of holotype, length 70 mm, Shattuck Zone 10, Calvert Formation (taken from Ward and Gilinsky, 1988, plate 1, figure 4). 6. *Ecphora (Ecphora) choptankensis vokesi* Petuch, 1989, ventral view of paratype, length 62 mm, Shattuck Zone 16, Choptank Formation. 7, 8. *Ecphora (Ecphora) turneri* n.sp., dorsal and ventral views of holotype, length (incomplete) 38 mm, UF 21465, Shattuck Zone 14, Calvert Formation. 9. *Ecphora (Triscephora) eccentrica* Petuch, 1989, dorsal view of paratype, length 56 mm, Shattuck Zone 10, Calvert Formation. 10. *Ecphora (Triscephora) scientistensis* n.sp., dorsal view of holotype, length (incomplete, fragmentary) 29 mm, UF 23799, Shattuck Zone 12, Calvert Formation. 11. *Ecphora (Triscephora) smithae* Petuch, 1988, dorsal view of paratype, length 75 mm, Shattuck Zone 16, Choptank Formation.

sis are tightly coiled and attached. The new species is confined to Shattuck Zone 12 of the Calvert Formation, Bed 12, Calvert.

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Parallel Development-Depth Trends in Deep-Sea Turrid Snails from the Eastern and Western North Atlantic

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Bouchet (1976a) first pointed out that a surprisingly high proportion of deep-sea prosobranchs bear larval shells that indicate planktotrophic development, a finding since supported by numerous surveys of deep-sea snail faunas (e.g. Bouchet and Warén, 1979, 1980, 1985; Rex and Warén, 1982; Colman *et al.*, 1986a). Studies using oocyte-size distributions (Rex *et al.*, 1979; Colman *et al.*, 1986b), stable isotope composition of larval and adult shells (Bouchet and Fontes, 1981; Killingley and Rex, 1985) and direct recovery of larvae from surface plankton and benthic egg capsules (Bouchet, 1976b; Bouchet and Warén, 1980; Gustafson *et al.*, 1991) have corroborated the use of larval shell morphology to infer mode of development, and revealed that planktotrophic larvae of some species undergo vertical migration in the water column. Both the frequency of planktotrophic development in deep-sea snails and ontogenetic vertical migration violate theoretical predictions about larval development in this cold, remote and nutrient-poor environment (Thorson, 1950; Vance, 1973). Rex and Warén (1982) showed that the incidence of planktotrophic development in prosobranchs actually increases with depth in the western North Atlantic. Bathymetric trends in developmental mode have not been analyzed in other regions of the deep sea to establish the generality of this pattern. Here, we compare development-depth trends between the eastern and western North Atlantic for the Turridae, the largest family of deep-sea prosobranchs.

The morphological criteria for determining the mode of larval development are particularly clear in turrids (Bouchet, 1990) and have been confirmed by direct observation in coastal representatives (e.g. Labour, 1934; Thorson, 1946; Thiriot-Quiévreux, 1972). Planktotrophic

larval shells have high spires, 2-5 whorls, brown color and fine reticulate or ribbed sculpture. The shell consists of two distinct parts: a minute Protoconch I at the apex which is deposited before hatching, and a larger Protoconch II grown during the planktotrophic phase of development (Robertson, 1974). Commonly, these larval shells are of the sinusigera type (Robertson, 1974) which have a distinctive beak on the aperture that projects between the velar lobes during the free-swimming stage. In contrast, shells of nonplanktotrophic larvae have a single bulbous whorl, are of the same white or gray color as the adult shell, and either lack visible sculpture or have very simple robust sculpture. Nonplanktotrophic larvae are provisioned with sufficient food to undergo development and hatch from benthic egg capsules. Though nonplanktotrophic larvae generally seem to have less dispersal potential than planktotrophic forms, the nonplanktotrophic larva of at least one turrid has a brief swimming phase after hatching and then lives demersally before metamorphosis (Shimek, 1986).

The two data sets compared are from Rex and Warén (1982) and Bouchet and Warén (1980) for the western and eastern North Atlantic respectively. We used only those species for which larval shells are known and which belong to genera included in the Turridae by Bouchet and Warén's taxonomic revision. This included 39 western species (80% with planktotrophic development) and 90 eastern species (74% with planktotrophic development). Rex and Warén (1982: Table 1) provide relative abundance data for species in 20 epibenthic sled samples collected from south of New England, whereas Bouchet and Warén report depth records for material from many sources included in their taxonomic revision. To make the two data bases more compatible, we determined the known depth range for each species in the separate regions, and calculated the percentage of species with planktotrophic development in each 500 m depth interval from the continental shelf to the abyssal plain. We then regressed the frequencies of planktotrophic devel-

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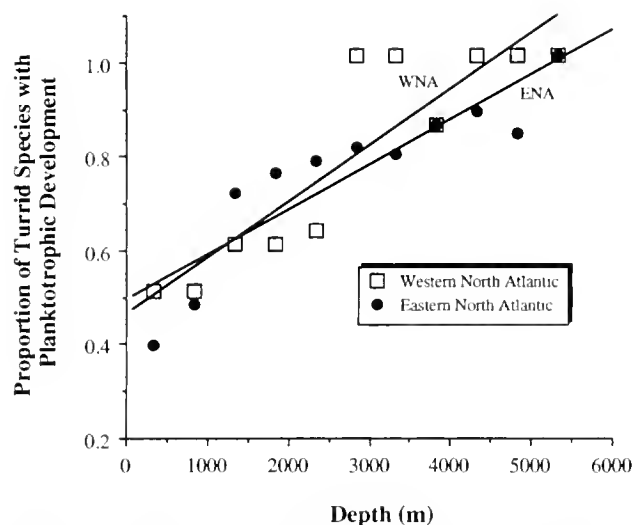


Figure 1. Relationships between the proportion of species with planktotrophic development in deep-sea turrid snails and depth, for the western (WNA) and eastern (ENA) North Atlantic. Regression equations and their statistics for WNA and ENA respectively are: $Y = 0.461 + 0.00012X$, $N=11$, $R^2 = 0.801$, $F = 36.155$, $P < 0.001$; $Y = 0.486 + 0.00010X$, $N=11$, $R^2 = 0.798$, $F = 35.476$, $P < 0.001$.

opment against depth, and performed an analysis of covariance (ANCOVA) to test for differences in slope and elevation of the development-depth relationships between the two regions.

Turrids from both regions show highly significant increases in the incidence of planktotrophic development with depth, and the trends are very similar (Figure 1; see caption for regression equations and their statistics). The ANCOVA reveals that the regressions for the eastern and western North Atlantic faunas are not statistically different in either slope ($F = 0.855$; d.f. = 1,18; n.s.) or elevation ($F = 0.952$; d.f. = 1,19; n.s.). When variables used in a regression are percentage values, such as here with the frequency of planktotrophy, arcsine transformations can be used to correct for departures from normality (Sokal and Rohlf, 1981). When this is done the regressions remain highly significant ($R^2 = 0.736$, $F = 25.040$, $N = 11$, $P < 0.001$; and $R^2 = 0.797$, $F = 35.406$, $N = 11$, $P < 0.001$ for western and eastern faunas respectively), and are still indistinguishable in slope ($F = 2.246$; d.f. = 1,18; n.s.) and elevation ($F = 3.688$; d.f. = 1,19; n.s.) by the ANCOVA. There are some idiosyncrasies in the trends. For example, there is a marked increase of about 40% in planktotrophy at 2500 m in the western fauna, and a large increment of about 20% at 1000 m in the eastern group (Figure 1). But overall, the two faunas show convincing increases in planktotrophic development with depth, and are remarkably alike in both the level of planktotrophy and its rate of increase with depth.

The analysis above suggests that a depth-related increase in the proportion of turrid species with plankto-

trophic development is widespread in the North Atlantic. It would be interesting to expand this research to include the proportion of endemic and shared species in eastern and western basins. This would enable us to explore, for example, whether horizontal geographic range is associated with mode of development (Jablonski and Lutz, 1983). We could also determine what proportion of the similarity in response shown in Figure 1 is attributable to shared and endemic components of the two faunas. At present, however, it is not possible to critically evaluate similarity in species composition on such large spatial scales. There has been no taxonomic synthesis of deep-sea turrids for the North Atlantic as a whole. Except for abundant and well-known species (see e.g. Etter and Rex, 1990), it is still unclear which species are actually common to both regions. Also, the large difference in the number of species represented in the two data bases places severe limitations on any calculated faunal similarity. The degree to which the two available species lists reflect a real shift in the regional diversity of turrids or merely the very substantial inter-regional difference in sampling intensity remains to be established.

It is intriguing that deep-sea turrids should have such a high proportion of species with planktotrophic development, and even show an increase in planktotrophy with depth, in an environment where nonplanktotrophic development appears to predominate in most taxa. Bouchet (1988) proposed that modes of larval development in deep-sea taxa, including snails, represent phylogenetic constraints, and are of no immediate adaptive significance. His arguments are especially compelling for groups like the archaeogastropods, which are found throughout the deep sea and have only nonplanktotrophic development. In these groups, larval development may be incidental to other adaptive features directly related to geographic distribution. In turrids, developmental mode is a fixed species-wide characteristic (Bouchet 1989, 1990). Planktotrophy is an ancestral condition that has been lost in many lineages, presumably during the course of speciation and adaptive radiation. The loss of feeding larvae in snails is potentially reversible (Strathmann, 1978), but there is no evidence that species have reacquired planktotrophic development during the evolutionary history of turrids (Bouchet, 1990).

However, while historical evolutionary events are responsible for establishing the overall developmental makeup of deep-sea snail assemblages, it is difficult to account for the clear and consistent depth trends shown in Figure 1 in purely nonadaptive terms. Environmental gradients associated with depth have caused marked bathymetric changes in the density (Rex *et al.*, 1990), species diversity (Rex, 1983) and species composition (Rex, 1977) of deep-sea snail faunas. Individual species also exhibit clinal effects with depth (Etter and Rex, 1990), particularly across the upper bathyal region where nonplanktotrophic development is more common (Figure 1). Depth-correlated selective gradients might be responsible for both driving the processes of population differentiation and speciation that ultimately generate

new species, and for actively maintaining their geographic distributions. Rex and Warén (1982) suggested two ways in which modes of larval development in turrids might be adaptively related to this selective gradient. Nonplanktrophic development might confer an advantage at upper bathyal depths because species' bathymetric and horizontal ranges are much more restricted there. Large-scale dispersal in ocean currents would carry planktrophic larvae away from adult habitats and limit successful recruitment. Conversely, selection may favor increased dispersal ability at greater depths to enable turrids to track progressively more rare and patchy prey resources.

Clearly, adaptation cannot provide a complete explanation for the trends shown in Figure 1, because species with planktrophic and nonplanktrophic development are found at all depths. Latitudinal gradients in the proportion of development types in prosobranchs (Thorson, 1950) present a similar problem of interpretation. Adaptation and phyletic constraint are both plausible hypotheses to account for part of the bathymetric variation in developmental modes of deep-sea turrids. Presently, it is not feasible to test these hypotheses experimentally by showing whether modes of development are adaptive to the ecological conditions at different depths in the sense that they actually improve fitness. However, a phylogenetic study of deep-sea turrids could demonstrate whether or not the same developmental modes have arisen independently in similar selective regimes.

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Drillia macleani, New Name for *Drillia sinuosa* McLean and Poorman, 1971 (Gastropoda: Turridae)

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During the preparation of a catalog of the family Turridae, I found the name *Drillia sinuosa* McLean and Poorman, 1971, which was applied to a Recent eastern pacific species, to be preoccupied by *Drillia sinuosa* Bellardi, 1877, which was applied to an unrelated species from the Middle Miocene of Italy. In order to rectify this homonymy and to acknowledge the seminal work on turrids done by the senior author of the preoccupied taxon, *Drillia macleani* is here proposed as a replacement name for the eastern Pacific species.

Drillia macleani Tucker, *nomen novum*

Drillia sinuosa McLean and Poorman, 1971:96, fig. 16., McLean in Keen, 1971:#1622.

Not *Drillia sinuosa* Bellardi, 1877:126, pl.4, figs. 18a,b.

Remarks: The holotype is in the collection of the Los Angeles County Museum of Natural History (LACM 1491). The type locality is off the southernmost coast of Isla Santa Cruz, Galápagos Islands, Ecuador (0°47'S, 90°21'W), in 150 m, collected 10 June 1968 by André and Jacqueline DeRoy.

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New Species of *Calliostoma* Swainson, 1840 (Gastropoda: Trochidae), and Notes on Some Poorly Known Species from the Western Atlantic Ocean

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ABSTRACT

Twenty-seven new species of *Calliostoma* Swainson (*sensu lato*) are described from the western Atlantic Ocean. *Trochus* (*Ziptyphinus*) *strophorus* Watson is confirmed to be a *Calliostoma*, with *C. arestum* Dall as a synonym, and *Trochus* (*Margarita*) *dnopherus* Watson is transferred to *Calliostoma*. New records and observations are presented for *C. apicinum* Dall, *C. indiana* Dall, *C. orion* Dall, *C. aurora* Dall, *C. fernandezi* Princz, *C. atlantis* Clench & Aguayo, *C. axelolssoni* Quinn (new name for *C. olssoni* Bayer), and *C. adspersum* (Philippi). External morphologies of the head-foot of 13 species are briefly described, and illustrations of the radulae of 13 species are presented, along with pertinent remarks.

Key words: Trochidae, Calliostomatinae, *Calliostoma*, systematics, new species, new records, radulae.

INTRODUCTION

The subfamily Calliostomatinae is by far the most speciose trochid subfamily in the western Atlantic Ocean. Species occur from the subarctic waters of Canada to the subantarctic waters of southern Argentina and the Antarctic waters of South Georgia Island (Powell, 1951; Clench & Turner, 1960). Calliostomatines inhabit a great variety of habitats, both biotic and abiotic, in depths ranging from the shallow subtidal to several hundred meters (Clench & Turner, 1960; Reed & Mikkelsen, 1987; Quinn, in press).

The greatest number of species of Calliostomatinae is assigned to the rather ill-defined genus *Calliostoma* Swainson, 1840. Clench and Turner (1960) monographed the western Atlantic species of the genus and concluded that 41 names represented valid species (including 5 new species), 24 names were synonyms, and 8 names were not referable to the genus. Subsequent studies (Merrill,

1970; Bayer, 1971; Princz, 1978; Quinn, 1979, in press; Rios, 1985, 1990) have revealed one new synonym and two new species, reinstated two species excluded by Clench and Turner, and resurrected three species from synonymy. Another 15 nominal species and subspecies not treated by Clench and Turner (1960) have been described from off southern Argentina (Philippi, 1845 [in 1842–1851]; Martens, 1881; Smith, 1881, 1915; Rochebrune & Mabilie, 1889; Strebel, 1905, 1908); a few of these species were discussed or mentioned by Powell (1951), who later (1960) published a complete list, but most of these species remain essentially unknown. Including the 27 new species described in this paper, the 2 here reassigned to the genus, and at least 7 that are currently unnamed, almost 100 valid Recent species of *Calliostoma* are now known from the western Atlantic (Table 1). In contrast, only 36 species of *Calliostoma* are known to occur in the eastern Pacific (Table 2) (see Dall, 1909; McLean, 1970, 1971, 1984; Rehder, 1971; McLean & Andrade, 1982). The number of valid Recent species of *Calliostoma* now known in the Americas is somewhat greater than the number of species described from the Neogene formations of the Americas.

At least six other calliostomatine species occur only off Argentina and in the Falkland and South Georgia Islands (Powell, 1951, 1960). Powell assigned two species each to *Falsimargarita* Powell, 1951, and *Photinastoma* Powell, 1951, and one species each to *Venustatrochus* Powell, 1951, and *Photinula* Adams and Adams, 1854. Clench and Turner (1960) assigned *Calliostoma blakei* Clench and Aguayo, 1938, to *Photinula*, but characters of the animal and radula show that the species should be assigned to the Lirulariinae Hickman and McLean, 1990 (Quinn, in preparation).

During the preparation of monographs of the Trochidae of the Gulf of Mexico (Quinn, in press) and the

adjoining Straits of Florida (Quinn, 1979). I examined specimens of many calliostomatine species collected from throughout the Caribbean Sea and southwestern Atlantic Ocean, most obtained subsequent to Clench and Turner's 1960 monograph. Many of the species represented in that material were clearly undescribed, some were found to be species complexes, and others represented significant range extensions of previously described but poorly known species. The purposes of this paper are to provide descriptions of the new species, to clarify the identities of some species, and to report new distributional data for species of *Calliostoma* in the western Atlantic Ocean. The external morphologies of the head-foot of 13 of the species are briefly described, and radulae of 13 species are illustrated. However, because so few species of western Atlantic *Calliostoma* have had their anatomy and radula illustrated, and because character states are so poorly understood for species worldwide, speculations on relationships based on the present observations are premature. Of particular interest would be optical microscope observations to clarify characteristics of these radulae as espoused by Hickman (1977).

Numerous genus-level taxa have been proposed for perceived species groups within Calliostomatinae. Although some authors incorporated features of the external anatomy and radula (e.g., Powell, 1951; Clench & Turner, 1960), most of these names were based on shell characters alone, and some names seem to reflect a regional bias of the authors; however, the morphological limits of these nominal taxa are nebulous, and a worldwide survey of genus-level taxa is needed. Therefore, the species discussed in the present paper are not formally assigned to nominal subgenera, but the following species groups are recognized as relatively distinct: the *C. pulchrum* group (*Calliostoma* s.s., or *Eucasta* Dall, 1889a); the *C. jujubinum* group (*Elmcrinia* Clench & Turner, 1960); the *C. bairdii* group (*Kombologion* Clench & Turner, 1960); the *C. sayanum* group; the *C. circumcinctum* group (?=*Otukaia* Ikebe, 1942); the *C. atlantis* group. Many western Atlantic species cannot be satisfactorily assigned to any species group, but a forthcoming revision of the southwestern Pacific calliostomatine species (B. A. Marshall, in litt.) may help clarify some of these uncertainties.

For brevity, authors and dates of publication for species included in Tables 1 and 2 are not repeated in the Remarks section of the species accounts. Species not included in those tables are cited with their authors and dates whenever mentioned in the text. Bibliographic references of species included in Tables 1 and 2 are not included in the Literature Cited section unless the species are also included in the text; most of these citations are readily available in Clench and Turner (1960), Keen (1971), and Quinn (in press).

Acronyms for specimen repositories are as follows: AMNH (American Museum of Natural History, New York); ANSP (Academy of Natural Sciences of Philadelphia); BM(NH) (The Natural History Museum, London); DMNH (Delaware Museum of Natural History,

Wilmington); FSBC I (Invertebrate Collection, Florida Marine Research Institute, St. Petersburg); HMNS (Houston Museum of Natural History, Texas); LACM (Natural History Museum of Los Angeles County, California); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts); MORG (Museu Oceanográfico da Fundação Universidade do Rio Grande, Rio Grande, Rio Grande do Sul, Brazil); UF (Florida Museum of Natural History, University of Florida, Gainesville); UMML (Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida); USNM (National Museum of Natural History, Smithsonian Institution, Washington, DC).

SYSTEMATICS

Superfamily Trochoidea Rafinesque, 1815

Family Trochidae Rafinesque, 1815

Subfamily Calliostomatinae Thiele, 1924

Genus *Calliostoma* Swainson, 1840

Type species (subsequent designation; Herrmannsen, 1846:154): *Trochus conulus* Linnaeus, 1758.

Calliostoma hilare new species
(figures 1, 2)

Description: Shell medium-sized, attaining height of 14.5 mm, width of 11.5 mm, conical, nonumbilicate, finely sculptured. Protoconch 375 μ m maximum diameter, 1 whorl. Teleoconch whorls 8.6, flat-sided; first whorl with weak axial riblets and 2 strong spiral cords; axial riblets disappearing on second whorl; spiral sculpture increasing by intercalation to 7 cords and 4 threads; suprapерipheral spiral cords finely beaded, beads crowded, rounded; periphery of first 4 whorls sharply carinate, composed of abapical spiral cord set with sharply conical beads, periphery of subsequent whorls narrowly rounded, composed of two adpressed spiral cords set with rounded beads. Base weakly convex, with 15 narrow, finely beaded spiral cords, cords becoming broader and more coarsely beaded adaxially. Aperture subquadrate, lips thin; columella almost straight, thickened, slightly twisted, terminating in weak, rounded denticle. Shell ground color golden yellow with greenish iridescence, with light golden brown and white spots alternating along periphery; white spots spirally elongate, brown spots axially elongate.

Holotype: USNM 860249, height 14.5 mm, width 11.5 mm.

Type locality: Off northwestern tip of Little Bahama Bank, JOHN ELLIOTT PILLSBURY Station P-198, 27°30'N, 79°10'W, in 242 m.

Distribution: This species is known only from the holotype, an empty shell, collected in 242 m off the northwestern tip of the Little Bahama Bank.

Remarks: The holotype of *C. hilare* is most similar to

Table 1. Geographic and bathymetric distributions of calliostomatine species in the western Atlantic Ocean.

Species	Depth (m)	Distribution
<i>Calliostoma</i> Swainson, 1840		
<i>jujubinum</i> (Gmelin, 1791)	0–10	4
<i>javanicum</i> (Lamarek, 1822)	0–40	4
<i>occidentale</i> (Mighels & A. Adams, 1842)	30–1,800	1, 2–
<i>gemmosum</i> (Reeve, 1842)	10–100	6
<i>nudum nudum</i> (Philippi, 1845)	?	7
<i>tampaense</i> (Conrad, 1846)	0–10	3–
<i>jucundum</i> (Gould, 1849)	20–30	7
<i>pulchrum</i> (C. B. Adams, 1850)	0–70	3, 4, 5, ?6
<i>adspersum</i> (Philippi, 1851)	0–40	5, 6
<i>euglyptum</i> (A. Adams, 1855)	10–30	3
<i>dnopherum</i> (Watson, 1879)	640	6*
<i>strophorum</i> (Watson, 1879)	700	3–, 4–
<i>coppingeri</i> Smith, 1880	10–80	6, 7
<i>bairdi</i> Verrill & Smith, 1880	70–450	2
<i>apicinum</i> Dall, 1881	100–200	4–
<i>circumcinctum</i> Dall, 1881	200–300	4–
<i>echinatum</i> Dall, 1881	70–150	4
<i>orion</i> Dall, 1881	20–60	4
<i>roscolum</i> Dall, 1881	40–80	3
<i>sapidum</i> Dall, 1881	100–250	?3–, 4
<i>yucatecanum</i> Dall, 1881	15–60	3
<i>consimilis</i> (Smith, 1881)	?	7
<i>aurora</i> Dall, 1888	180–1,050	4
<i>benedicti</i> Dall, 1889	365	3–*
<i>brunneum</i> (Dall, 1889)	20–70	4
<i>cinctellum</i> Dall, 1889	?–300	3–, 4*
<i>indiana</i> Dall, 1889	50–100	4
<i>psyche</i> Dall, 1889	100–400	3–
<i>sayanum</i> Dall, 1889	150–300	3–
<i>dozei</i> Rochebrune & Mabilie, 1889	?	7
<i>nudum roseotinctum</i> Rochebrune & Mabilie, 1889	?	7
<i>optimum</i> Rochebrune & Mabilie, 1889	?	7
<i>senius</i> Rochebrune & Mabilie, 1889	?	7
<i>irisans</i> Strebel, 1905	?	7
<i>kophameki</i> Strebel, 1905	?	7
<i>moebiusi</i> Strebel, 1905	90	7
<i>nudum flavidocornea</i> Strebel, 1905	?	7
<i>marionae</i> Dall, 1906	40–120	3
<i>militare</i> Ihering, 1907	30–65	6, 7
<i>andersoni</i> Strebel, 1908	?	7
<i>falklandicum</i> Strebel, 1908	15–250	7
<i>modestulum</i> Strebel, 1908	65–350	7
<i>nordenskjoldi</i> Strebel, 1908	?	7
<i>venustum</i> Strebel, 1908	40	7
<i>depictum</i> Dall, 1927	1–7	6
<i>halibreetum</i> Dall, 1927	535	3*
<i>hendersoni</i> Dall, 1927	150–350	3–
<i>sarcodum</i> Dall, 1927	1–10	4
<i>amazonicum</i> Finlay, 1930	?	7
<i>bigelowi</i> Clench & Aguayo, 1938	375–430	4*
<i>schroederi</i> Clench & Aguayo, 1938	250–450	4–
<i>hassler</i> Clench & Aguayo, 1939	65	6*
<i>atlantis</i> Clench & Aguayo, 1940	?–600	4–
<i>carcellesi</i> Clench & Aguayo, 1940	50	7*
<i>cubanum</i> Clench & Aguayo, 1940	900	4*
<i>torrei</i> Clench & Aguayo, 1940	700	4*
<i>fascians</i> Schwengel & McGinty, 1942	70–120	3
<i>barbouri</i> Clench & Aguayo, 1946	25–100	3–, 4
<i>adela</i> Schwengel, 1951	0–2	3–
<i>bullisi</i> Clench & Turner, 1960	70	5*

Table 1. Continued

Species	Depth (m)	Distribution
<i>jeanneae</i> Clench & Turner, 1960	?	4*
<i>oregon</i> Clench & Turner, 1960	200–350	3–
<i>rosewateri</i> Clench & Turner, 1960	274–641	4–
<i>springeri</i> Clench & Turner, 1960	200–450	3–
<i>fernandezii</i> Princz, 1978	45–145	5
<i>alternum</i> Quinn, 1992	55–146	5
<i>argentum</i> Quinn, 1992	350–450	4
<i>atlantoides</i> Quinn, 1992	400–600	4*
<i>aulicum</i> Quinn, 1992	10–50	5
<i>axelssonii</i> Quinn, 1992	200–300	4–, 6–
<i>bermudense</i> Quinn, 1992	82	3*
<i>brunneopictum</i> Quinn, 1992	50–80	6*
<i>cnidophilum</i> Quinn, 1992	150–350	3
<i>coronatum</i> Quinn, 1992	770–800	6*
<i>cubense</i> Quinn, 1992	0–20	4–
<i>debile</i> Quinn, 1992	?	4*
<i>dentatum</i> Quinn, 1992	15–55	3–
<i>fucosum</i> Quinn, 1992	5–9	5*
<i>guesti</i> Quinn, 1992	183–219	4*
<i>hilaris</i> Quinn, 1992	250	4*
<i>hirtum</i> Quinn, 1992	520	4*
<i>moscatellii</i> Quinn, 1992	50–80	6
<i>purpureum</i> Quinn, 1992	0–60	5–
<i>rota</i> Quinn, 1992	27	6*
<i>rude</i> Quinn, 1992	60–90	5–
<i>rugosum</i> Quinn, 1992	?	4*
<i>scalenum</i> Quinn, 1992	25–80	3
<i>scurra</i> Quinn, 1992	20–90	5
<i>semisuaire</i> Quinn, 1992	70–155	5–
<i>serratulum</i> Quinn, 1992	120–190	5–
<i>tenebrosus</i> Quinn, 1992	?	6*
<i>vinosum</i> Quinn, 1992	18–22	6
<i>viscardii</i> Quinn, 1992	40–45	6*
<i>Venustatrochus</i> Powell, 1951		
<i>georgianus</i> Powell, 1951	120–200	7*
<i>Falsimargarita</i> Powell, 1951		
<i>gemma</i> (Smith, 1915)	200–400	8
<i>iris</i> (Smith, 1915)	225–450	7
<i>Photinula</i> Adams & Adams, 1854		
<i>coerulescens</i> (King & Broderip, 1831)	0–200	7
<i>Photinastoma</i> Powell, 1951		
<i>taeniata taeniata</i> (Wood, 1828)	0–80	7
<i>taeniata nivea</i> (Cooper & Preston, 1910)	0–100	7*
? <i>gamma</i> (Rochebrune & Mabile, 1889)	?	7

* Known only from the type lot or locality; 1 = northern boreal, 2 = "Virginian" (Cape Cod to Cape Hatteras); 3 = Carolinian; 4 = Caribbean; 5 = northern South America, 6 = Brazil–northern Argentina; 7 = Patagonian; 8 = Subantarctic; "–" indicates restricted range within region

shells of *C. rude* in shape, size, and sculpture, but it differs by having a slightly larger protoconch (375 μ m vs. 350 μ m); by having the peripheral spiral cord strong and sharply beaded on whorls 2–4, becoming weaker and with rounded beads on later whorls, whereas the peripheral cord of *C. rude* is inconspicuous on the first three whorls, becoming very strong and coarsely beaded on subsequent whorls; and by having more numerous

but weaker spiral cords. *Calliostoma hilaris* is also similar to *C. serratulum*, but the shell of the former has a smaller protoconch (375 μ m vs. 400–425 μ m), is proportionately narrower, has more numerous spiral cords that are more weakly beaded, and has a periphery that is composed of two subequal, finely beaded, adpressed cords rather than a strong, coarsely beaded upper cord and a weaker lower cord.

Table 2. Geographic and bathymetric distributions of calliostomatine species in the eastern Pacific Ocean.

Species	Depth (m)	Distribution
<i>Calliostoma</i> Swainson, 1840		
<i>annulatum</i> (Lightfoot, 1786)	"offshore"	1
<i>canaliculatum</i> (Lightfoot, 1786)	25–750	1
<i>antonii</i> (Koch, 1843)	0–3	3
<i>eximium</i> (Reeve, 1843)	0–40	3
<i>ligatum</i> (Gould, 1849)	0–3	1
<i>leanum</i> (C. B. Adams, 1852)	0–3	3
<i>foukii</i> (Philippi, 1860)	?–457	3, 4
<i>gemmulatum</i> Carpenter, 1864	0–3	2
<i>splendens</i> Carpenter, 1864	"offshore"	2
<i>supragranosum</i> Carpenter, 1864	0–3	2
<i>variegatum</i> Carpenter, 1864	25–750	1
<i>acquisculptum</i> Carpenter, 1865	1–3	3
<i>tricolor</i> Gabb, 1865	15–60	2, 3
<i>gloriosum</i> Dall, 1871	0–40	2
<i>palmeri</i> Dall, 1871	0–45	3
<i>platinum</i> Dall, 1890	80–750	1
<i>turbinum</i> Dall, 1895	60–120	2
<i>iridium</i> Dall, 1896	230–280	3
<i>nepheloide</i> Dall, 1913	50–125	3
<i>bonita</i> Strong, Hanna, & Hertlein, 1933	35–75	3
<i>rema</i> Strong, Hanna, & Hertlein, 1933	20–45	3
<i>marshalli</i> Lowe, 1935	0–3, "offshore"	3
<i>mcleani</i> Shasky & Campbell, 1964	5–10	3
<i>gordanum</i> McLean, 1970	128	2*
<i>jacquelineae</i> McLean, 1970	146	3*
<i>keenae</i> McLean, 1970	55–110	2, 3
<i>sanjaimense</i> McLean, 1970	137	2*
<i>santacruzianum</i> McLean, 1970	45	3*
<i>celeroae</i> McLean, 1970	60–100	3
<i>insignis</i> Olsson, 1971	50–80	3
<i>joannae</i> Olsson, 1971	53	3*
<i>pillsburyae</i> Olsson, 1971	57–64	3*
<i>chilena</i> Rehder, 1971	200–750	3, 4
<i>delhi</i> McLean & Andrade, 1982	200–450	4–
<i>bernardi</i> McLean, 1984	125–175	1
<i>titanium</i> McLean, 1984	200–300	2–

* Known only from the type lot or locality; 1 = northern boreal; 2 = Californian; 3 = Panamic; 4 = Peruvian; "–" indicates restricted range within region

Calliostoma serratulum new species
(figures 3–6)

Calliostoma sp. 4 Bayer *et al.*, 1970:A29, A137, A146

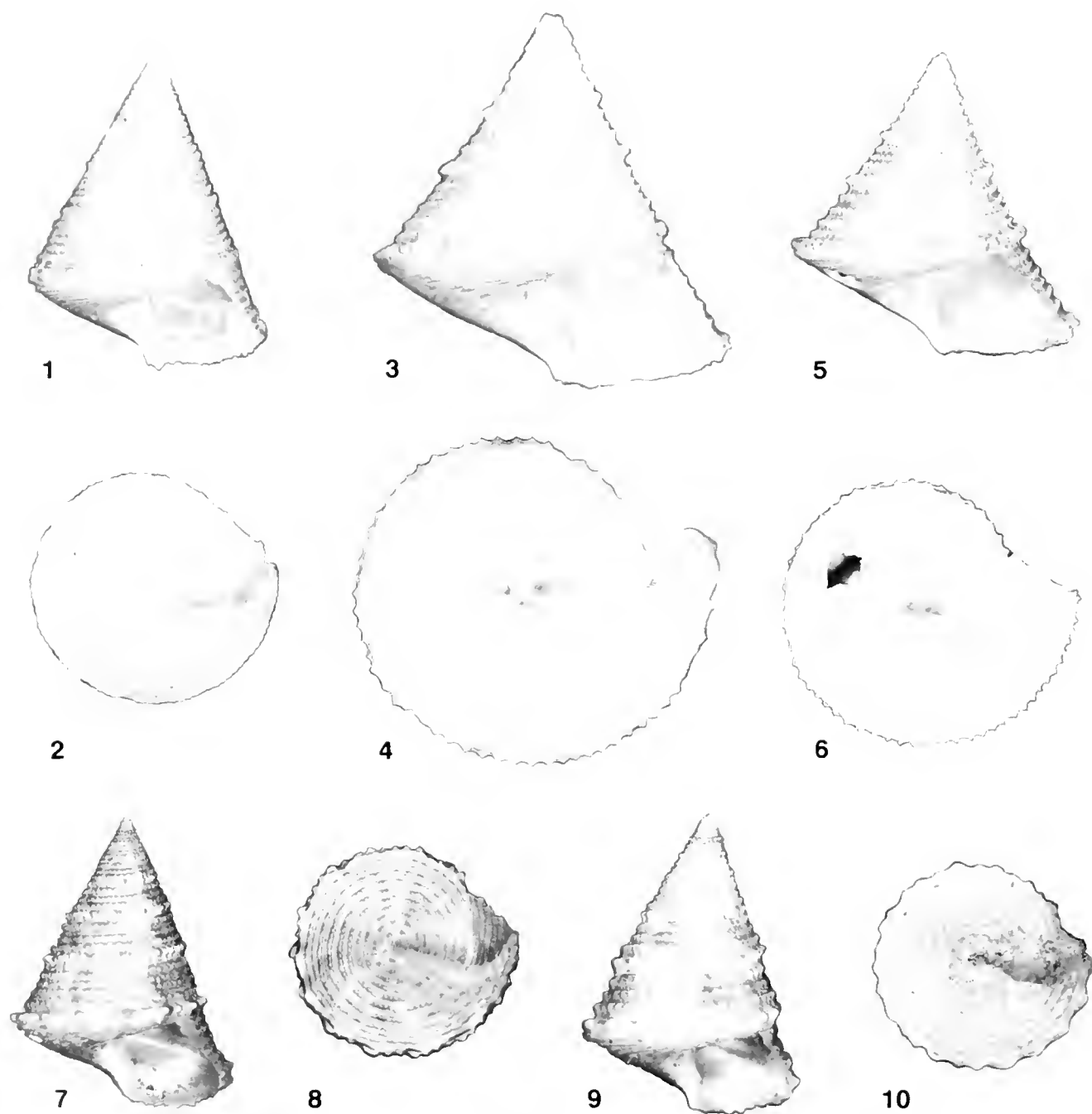
Description: Shell medium-sized, attaining height of 16.7 mm, width of 16.4 mm, conical, nonumbilicate, coarsely sculptured. Protoconch 400–425 μ m maximum diameter, 1 whorl. Teleoconch whorls about 7, flat; first 2 whorls with low, rounded axial riblets and 2 strong, beaded spiral cords; axial riblets gradually disappearing on whorls 3–5; spiral sculpture increasing by intercalation to 5–8 cords and 0–5 threads, of which abapical 2 cords forming periphery; periphery sharply carinate; adapical peripheral cord strong, projecting, set with strong, conical beads, beads crossed by 2 fine spiral threads producing squarish apices; abapical peripheral cord weaker, weakly beaded. Base weakly convex, with 13–17 narrow, weakly beaded spiral cords, adaxial 2–3 cords

stronger, more widely spaced, and more distinctly beaded. Aperture subquadrate, lips thin, weakly crenulate; columella concave above, straight below, thickened, terminating in weak, rounded denticle. Shell ground color golden yellow with spots and axial streaks of brown; beads white; basal spiral cords with elongate spots of brown, darkest on adaxial 2–3 cords.

Holotype: USNM 860250, height 12.5+ mm, width 12.3 mm.

Type locality: Southwest of Cartagena, Colombia, JOHN ELLIOTT PILLSBURY Station P-375, 9°59.0'N, 76°02.0'W, in 135–130 m.

Paratypes: 1, UMML 30.3539, off Santa Marta, Colombia, JOHN ELLIOTT PILLSBURY Station P-399, 9°01.3'N, 76°40.2'W, 119–179 m; 17 July 1966; 10-ft otter trawl.—1, UMML 30.6935; 1, FSBC 1 44069; off Península de



Figures 1, 2. *Calliostoma hularc* new species, holotype, USNM 860249; height 14.5 mm, width 11.5 mm. Figures 3–6. *Calliostoma serratulum* new species. 3, 4. Holotype, USNM 860250, height 12.5+ mm, width 12.3 mm. 5, 6. Paratype, UMML 30.3539; height 10.1 mm, width 10.0 mm. Figures 7, 8. *Calliostoma rude* new species, holotype, USNM 860251, height 13.3 mm, width 10.6 mm. Figures 9, 10. *Calliostoma* sp. cf. *rude*, specimen from off Barbados, Sunderland collection, height 9.7 mm, width 7.3 mm.

Paraguaná, Venezuela, JOHN ELLIOTT PILLSBURY Station P-757, 11°39.6'N, 69°22.1'W, 161–187 m; 27 July 1968; 10-ft otter trawl.

Other material: 4 broken, UMML 30.8366, off Santa Marta, Colombia, JOHN ELLIOTT PILLSBURY Station P-785, 11°16.9'N, 74°17.0'W, 176–165 m; 31 July 1968; 10-ft otter trawl.

Distribution: *Calliostoma serratulum* is known only from empty shells trawled from off the northeastern coast of Colombia and northwestern coast of Venezuela in 119–187 m.

Remarks: Shells of *C. serratulum* are most similar to those of *C. rude* but differ by having a much larger protoconch (400–425 μ m vs. 350 μ m), by being propor-

tionately wider, and by having the adapical peripheral cord set with uniformly sized beads that are squarish in profile.

Calliostoma rude new species

(figures 7, 8)

Description: Shell medium-sized, attaining height of 13.3 mm, width of 10.6 mm, conical, nonumbilicate, coarsely sculptured. Protoconch 350 μ m maximum diameter, 1 whorl. Teleoconch whorls 8.3, flat; first whorl with low, rounded axial riblets and 2 strong, beaded spiral cords; axial sculpture absent after first whorl; spiral sculpture increasing by intercalation to 5–6 cords and 1–2 threads, of which abapical 2 cords forming periphery; periphery sharply carinate; adapical peripheral cord strong, strongly beaded, beads triangular, every third or fourth bead markedly larger; abapical peripheral cord weaker, strongly undulate. Base weakly convex, with 11–13 strong, narrow, finely beaded spiral cords. Aperture subquadrate, lips thin, finely crenulate; columella almost straight, thickened, terminating in weak, rounded denticle. Shell ground color ivory with greenish and reddish iridescence; streaks and flammules of golden brown present above periphery; periphery with spots of darker brown; base with light golden-brown spots arranged on cords to form obscure, crescentic radial streaks.

Holotype: USNM 860251, height 13.3 mm, width 10.6 mm

Type locality: Off Cayenne, French Guiana, JOHN ELLIOTT PILLSBURY Station P-650, 6°07.0'N, 52°19.0'W, in 84–91 m.

Paratypes: 2, UMML 30.5844; 1, FSBC I 44076; from same lot as holotype.—2, MCZ 302593; off Georgetown, Guyana, CHAIN Cruise 35, Station 35+36, 8°10.5'–8°10.0'N, 57°48'W, 53–60 m; 28 April 1963.

Distribution: *Calliostoma rude* is known only from two collections, one off Georgetown, Guyana, in 53–60 m, and the other from the type locality off Cayenne, French Guiana, in 84–91 m; the latter collection contained a single live-collected specimen. The field notes on the type locality cite shell rubble, and the associated invertebrates suggest that hard-bottom outcrops are nearby.

Remarks: Comparisons of shells of *Calliostoma rude* with those of the similar *C. serratum* and *C. hilare* are discussed in the remarks for the latter two species. The adapical peripheral cord of shells of *C. rude* is subequal to the other spiral cords on the first three whorls, but it becomes markedly stronger on the fourth and subsequent whorls. This characteristic separates *C. rude* from all other peripherally carinate species in which peripheral carination is present on the first whorls and either remains strong on all whorls (e.g., *C. cinctellum*) or disappears on the last one or two whorls (e.g., *C. echinatum*). The alternation of two or three small beads with a much larger triangular bead is also unique to *C. rude*. Four specimens collected from off the western coast

of Barbados (Figures 9, 10; Sunderland collection, ex F. Sander) are very similar to the types of *C. rude* but are relatively smaller and narrower and have some subtle sculptural differences that suggest that the Barbados shells may be a separate species.

Calliostoma cnidophilum new species

(figures 11–14, 107)

Description: Shell medium-sized, attaining height of 14.1 mm, width of 12.1 mm, conical, nonumbilicate, finely sculptured. Protoconch 375 μ m maximum diameter, 1 whorl. Teleoconch whorls about 8, flat; first whorl with low, rounded axial riblets and 2 strong, beaded spiral cords; axial riblets disappearing on second whorl; spiral sculpture increasing by intercalation to 10–12 cords and 0–2 threads, cords finely beaded; periphery of first 2–2.5 whorls sharply carinate, set with sharply conical beads; periphery becoming narrowly rounded on subsequent whorls, beads becoming finer, rounded; peripheral cord splitting into 2 subequal, adpressed cords on fifth whorl; periphery obscurely multiangulate when viewed from base. Base weakly convex, with 14–20 narrow, sharp, very finely beaded spiral cords. Aperture subquadrate, lips thin, finely crenulate; columella short, weakly concave, thickened. Shell ground color golden yellow with greenish iridescence; periphery with regularly spaced, spirally elongate pinkish spots. Animal (in alcohol) white; cephalic tentacles long, slender, gradually tapering, right longer than left, ocular peduncles long, slender, with large, black eye at tips; epipodium with 4 pairs of tentacles decreasing in size posteriorly, neck lobes well-developed, thin, semicircular, smooth.

Holotype: USNM 860265, height 13.7 mm, width 11.4 mm.

Type locality: Off Îlets-à-Goyaves, Guadeloupe, Lesser Antilles, JOHNSON-SEA-LINK II Station JSL-II-1845, 16°10'00"N, 61°49'08"W, in 306 m.

Paratypes: 2, UMML 30.8370; 1, FSBC I 44070; off Dominica, JOHN ELLIOTT PILLSBURY Station P-931, 15°31.2'N, 61°12.3'W, 174–357 m; 15 July 1969; 5-ft Blake trawl.

Other material: 1, Sunderland collection; off St. James, Barbados, 152 m; ex F. Sander.

Distribution: *Calliostoma cnidophilum* is known from the Lesser Antilles in depths of 152–357 m; living specimens were collected in 306 m and 174–357 m.

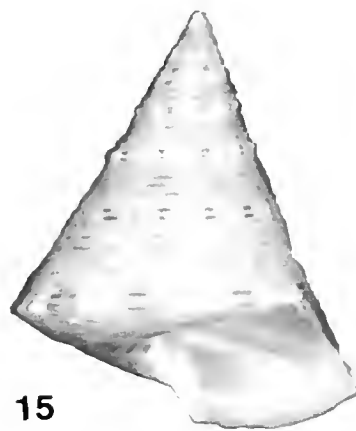
Remarks: Shells of *Calliostoma cnidophilum* are most similar to the holotype of *C. hilare* but differ by being proportionately broader; by having an obscurely multiangulate peripheral profile when viewed from the base; by having finer, more numerous spiral cords above the periphery; by having the spiral cords more finely beaded; and by having a shorter, thicker columella. The radula (formula $\infty.5.1.5.\infty$; figure 107) differs from that illustrated by Clench and Turner for *C. pulchrum* (1960:pl.



11



13



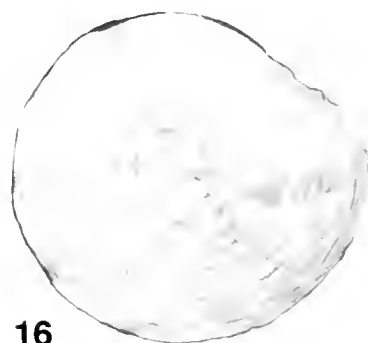
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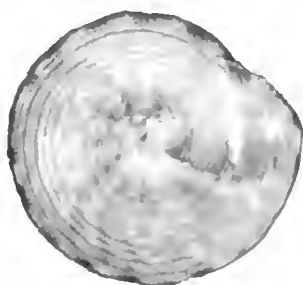
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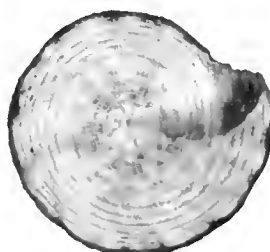
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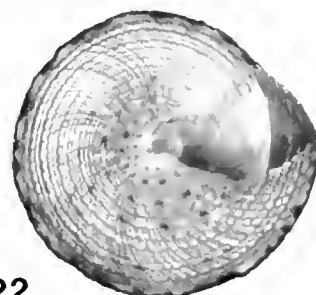
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22

3, fig. 3) by having the rachidian teeth with much broader bases and cusps and by having narrower cusps on the lateral teeth.

Observations made from the submersible JOHNSON-SEA-LINK II indicate that *C. cnidophilum* may feed on octocorals (M. G. Harasewych, personal communication; see also Harasewych *et al.*, 1992, fig. 12).

Calliostoma semisuave new species
(figures 15, 16)

Description: Shell medium-sized, attaining height of 13.4 mm, width of 11.4 mm, conical, nonumbilicate, finely sculptured. Protoconch 400 μ m maximum diameter, 1 whorl. Teleoconch whorls 8.5, flat; first 4 whorls with low, rounded axial riblets and 2–4 strong beaded spiral cords; axial sculpture disappearing on fifth whorl; spiral sculpture increasing by intercalation to 11 cords and 2–3 threads, cords strongly beaded on first 5 whorls, beads gradually weakening on subsequent whorls; periphery sharply carinate, with single strong, smooth, peripheral cord. Base weakly convex, with 16–18 narrow, smooth to very weakly beaded spiral cords. Aperture subquadrate, lips thin; columella almost straight, thickened, terminating in sharp denticle. Shell ground color cream to light golden yellow, with diffuse spots and flammules of light golden brown; periphery with distinct, squarish spots of orange-brown.

Holotype: USNM 860252, height 13.4 mm, width 11.4 mm.

Type locality: West of Isla La Tortuga, Venezuela, JOHN ELLIOTT PILLSBURY Station P-736, 10°57.0'N, 65°52.0'W, in 69–155 m.

Paratype: 1, UMMIL 30.5915; off Pointe Isère, French Guiana, JOHN ELLIOTT PILLSBURY Station P-638, 7°10.0'N, 53°36.0'W, in 135–126 m; 9 July 1968; 10-ft otter trawl.

Distribution: *Calliostoma semisuave* is known from dead shells collected off eastern Venezuela and northwestern French Guiana in depths of 69–155 m.

Remarks: The shells of *Calliostoma semisuave* are most similar to those of *C. cnidophilum* but are proportionately narrower, have a larger protoconch, have the beading of the spiral cords becoming very weak on the last several whorls, and have a smooth peripheral cord on the last several whorls.

Other organisms listed on the field data sheets for the two collections of *C. semisuave* include sponges, alcyonarians, *Millepora*, *Haliotis*, and chitons, suggesting that this species lives on or near hard-bottom outcrops in depths of about 70–150 m.

Calliostoma brunneopictum new species
(figures 17–20)

Description: Shell small, attaining height of 8.5 mm, width of 6.9 mm, conical, narrowly umbilicate or non-umbilicate, finely sculptured. Protoconch 365–375 μ m maximum diameter, 1 whorl. Teleoconch whorls 6.7, flat to weakly convex; first whorl with low, rounded axial riblets and 2 strong, beaded spiral cords; axial sculpture absent after first whorl; spiral sculpture increasing by intercalation to 8–12 cords and 1–3 threads, cords finely beaded, beads conical; periphery rather sharp on first 5 whorls, becoming narrowly rounded on last 2 whorls. Base weakly convex, with 12–16 narrow, finely beaded spiral cords, adaxial 2–3 cords slightly stronger and more widely spaced. Umbilicus very narrow, chink-like, partially or completely filled by columella. Aperture subquadrate to subovate, lips thin, finely crenulate; columella concave, thickened, terminating in obscure, rounded denticle. Shell ground color ivory with greenish and reddish iridescence, irregular spots and flammules of brown above periphery, squarish spots of brown regularly spaced on periphery, and obscure, crescentic streaks of brown on base.

Holotype: MORG 29.291, height 8.5 mm, width 6.9 mm.

Type locality: Off Santana Island, Estado de Rio de Janeiro, Brazil, in 50–80 m.

Paratypes: 1, MCZ 302592; 1, FSBC I 44068; from same lot as holotype.

Other material: 2, Coltro collection; from same lot as holotype.—1, Sunderland collection; off Rio de Janeiro, Brazil, 50–70 m; trawled by shrimpers.

Distribution: At present, *Calliostoma brunneopictum* is known only from off Rio de Janeiro, Brazil, in depths of 50–80 m. Living specimens are also known from 50–80 m.

Remarks: Shells of *Calliostoma brunneopictum* are most similar to those of *C. roscolum* but differ by having a larger protoconch (365–375 μ m vs. 325 μ m); by having more numerous, more finely beaded spiral cords; by having an umbilical chink; and by having crescentic streaks of brown on the base. Differences between *C. brunneopictum* and the similar *C. viscardii* are discussed in the Remarks section of the latter species.

Calliostoma viscardii new species
(figures 21, 22, 108)

Figures 11–14. *Calliostoma cnidophilum* new species. **11, 12.** Holotype, USNM 860265; height 13.7 mm, width 11.4 mm. **13, 14.** Specimen from off Barbados, Sunderland collection; height 11.2 mm, width 9.2 mm. **Figures 15, 16.** *Calliostoma semisuave* new species, holotype, USNM 860252; height 13.4 mm, width 11.4 mm. **Figures 16–20.** *Calliostoma brunneopictum* new species. **17, 18.** Holotype, MORG 29.291; height 8.5 mm, width 6.9 mm. **19, 20.** Paratype, FSBC I 44068; height 7.5 mm, width 6.0 mm. **Figures 21, 22.** *Calliostoma viscardii* new species, holotype, MORG 29.292; height 10.9 mm, width 8.2 mm.

Description: Shell small to medium-sized, attaining height of 13.0 mm, width of 10.8 mm, conical, non-umbilicate, finely sculptured. Protoconch 300–335 μm maximum diameter, 1 whorl, tip violet. Teleoconch whorls 8.25, flat to weakly convex; first whorl with 2 strong, smooth to weakly beaded spiral cords, initially lacking axial sculpture but developing low, rounded riblets near end of whorl, riblets persisting on subsequent whorls as low folds between spiral cords; spiral sculpture increasing by intercalation to 7–8 cords and 2–6 threads, of which abapical 2 spiral cords forming periphery, cords rather coarsely beaded, beads rounded, slightly spirally elongate on last 2 whorls; periphery rather sharp on first 5 whorls, becoming narrowly rounded on last 2 whorls, peripheral cords adpressed. Base weakly convex, with 13–16 narrow, weakly beaded spiral cords. Aperture subquadrate to subovate, lips thin, finely crenulate; columella concave, thickened, terminating in obscure, rounded denticle. Shell ground color tan with greenish and reddish iridescence, patches and flammules of brown and occasional white spots on and above periphery, and elongate spots of brown on basal cords. Animal (in alcohol): foot dark brown with white papillae; mantle edge with irregular band of brown, mantle mottled black and white posteriorly; head mottled black and white; cephalic tentacles short, stout, tapering rapidly to narrow tip; eye-stalks short (but about 40% tentacle length), stout, with large, black eye at tips; snout mottled with brown and white, longer than broad, slightly longer than cephalic tentacles, slightly tapered at tip, tip with fringe of fine, rather long papillae; epipodium with 4 pairs of short, stout tentacles; left neck lobe seems to be smooth, right lobe finely digitate.

Holotype: MORG 29.292, height 10.9 mm, width 8.2 mm.

Type locality: Between Ilha de São Sebastião and Ilha de Buzias, off São Paulo, Estado de São Paulo, Brazil, in 40–45 m.

Paratypes: 1, USNM 860253; 1, FSBC 1 44066; from same lot as holotype.

Other material: 3, Coltro collection; off Guarapari, Estado de Espírito Santo, Brazil, 20–30 m; trawl; July 1991.—6, Coltro collection; off Ilha de São Sebastião, Estado de São Paulo, Brazil, 30–35 m; dredge; J. & M. Coltro & L. F. Viscardi, collectors.

Distribution: *Calliostoma viscardii* is known from southeastern Brazil (Guarapari to São Paulo) in depths of 20–45 m; living specimens have been collected in depths of 30–45 m.

Remarks: Shells of this species resemble those of *Calliostoma brunneopictum* but differ by having a smaller protoconch (300–335 μm vs. 365–375 μm) with a violet tip; by having stronger, more widely spaced spiral cords whose beads are large and rounded rather than small and conical; by having the whorl periphery composed of a pair of close-set spiral cords abapical to the cord

that is the continuation of the abapical cord on the first whorl, whereas the abapical cord on the first whorl of *C. brunneopictum* forms the periphery on all whorls; and by having less well-defined beading on the basal spiral cords. *Calliostoma viscardii* is also similar to *C. roseolum*, but the shells have a larger protoconch (335–350 μm vs. 300–335 μm); lack the prominent, broadly rounded whorl periphery; have stronger, more widely spaced spiral cords above the periphery; and have slightly larger but less discrete beading. The radula of *C. viscardii* (formula $\infty.5.1.5.\infty$; figure 108) does not differ significantly from that of *C. pulchrum* illustrated by Clench and Turner (1960:pl. 3, fig. 3).

This species is named *viscardii* to recognize the contributions of Sr. Luiz Francisco Viscardi to Brazilian malacology.

Calliostoma bermudense new species
(figures 23, 24)

Description: Shell small to medium-sized, attaining height of 12.6 mm, width of 8.9 mm, conical, nonumbilicate, finely sculptured. Protoconch 315–325 μm maximum diameter, 1 whorl. Teleoconch whorls about 8, flat to weakly concave; first whorl with low, rounded axial riblets and 2 strong, beaded spiral cords; axial sculpture weakening rapidly at end of second whorl, absent thereafter; spiral sculpture increasing by intercalation to 8–10 cords and 1–4 threads, of which abapical 2–3 cords forming periphery, cords strongly beaded; periphery of first 3–4 whorls sharply angulate, that of subsequent whorls broadly rounded, not distinctly set off from base. Base flat to weakly convex, with 10–14 narrow, weakly beaded spiral cords of which 1–3 markedly weaker. Aperture subquadrate to ovate, thickened within, lips thin, crenulate; columella short, almost straight, thickened. Shell ground color yellowish brown, spiral cords brown, often broken into dashed lines on base, periphery often with diffuse patches of brown to red-brown, apical 3–4 whorls pinkish brown.

Holotype: DMNH 187591, height 11.9 mm, width 8.9 mm.

Type locality: Off Castle Roads, Bermuda, in 82 m.

Paratypes: 9, DMNH 187592; 2, USNM 860269; 1, FSBC 1 42541; all from same lot as holotype.

Distribution: *Calliostoma bermudense* is known only from the type locality; no living specimens are known.

Remarks: Shells of *Calliostoma bermudense* are most similar to those of *C. roseolum* but differ by being relatively broader; by having narrower, more widely spaced and more finely beaded spiral cords; by having a flatter whorl profile after the fourth whorl; by having a proportionately shorter and thicker columella; by having brown or pinkish-brown apical whorls; and by having brown spiral cords.

Calliostoma dentatum new species
(figures 25, 26)

Description: Shell small, attaining height of 8.4 mm, width of 7.4 mm, conical, nonumbilicate, finely sculptured. Protoconch 335–350 μm maximum diameter, 1 whorl. Teleoconch whorls 8, flat to weakly concave; first 2 whorls with low, rounded axial riblets and 2 strong, beaded spiral cords; axial sculpture on remaining whorls of low, rounded, discontinuous axial threads, most distinct at periphery; spiral sculpture increasing by intercalation to 4–8 strongly beaded cords, of which abapical 2–3 spiral cords forming periphery; periphery angulate, adapical peripheral cord strongest, abapical 2 (when 3 present) weaker, closely appressed, set with axially elongate beads. Base flat, with 10–14 narrow, finely beaded spiral cords. Aperture subquadrate, lips thin, crenulate; columella straight, thickened. Shell ground color ivory with diffuse axial flammules of golden brown above periphery, and 2–3 spiral rows of discrete, spirally elongate spots of golden or reddish brown on base.

Holotype: USNM 859358, height 5.7 mm, width 5.2 mm.

Type locality: Off Freeport, Texas, approximately 28°05'N, 94°35'W, in 51 m.

Paratypes: 1, MCZ 297052; 1, LACM 2293; 1, HMNS 3946; NW Gulf Survey station, off Freeport, Texas, 51 m; trawl; A. Kight, collector.—1, HMNS 15866; 2, FSBC 132301; NW Gulf Survey station, 2 mi south of #1 buoy, Heald Bank, 22 m; 22 August 1966; H. Geis and W. Pierce, collectors. Other paratypes and material (44 lots) are listed by Quinn (in press).

Distribution: *Calliostoma dentatum* is confined to the northwestern Gulf of Mexico, from the Mississippi River to off Port Isabel, Texas, and is usually collected from depths of 15–55 m; living specimens are known from depths of 12–51 m.

Remarks: *Calliostoma dentatum* is closely related to *C. pulchrum*, *C. roseolum*, and the Plio-Pleistocene *C. bowdenense* Woodring, 1928. Shells of *C. dentatum* differ from those of *C. pulchrum* by having a larger protoconch \bar{x} = 346 μm vs. 300 μm ; Quinn, in press); by having fewer spiral cords both above and below the periphery; and by having the beads on the cords stronger, more sharply defined, and laterally compressed. Shells of *C. dentatum* differ from those of *C. roseolum* by having a larger protoconch \bar{x} = 346 μm vs. 324 μm), by being relatively narrower, by having a narrower and more angulate periphery, and by having laterally compressed beads on the spiral cords. Shells of *C. dentatum* differ from those of *C. bowdenense* by having more numerous spiral cords above the periphery; by having a narrower, more sharply angulate periphery; and by having weaker, more weakly beaded spiral cords on the base. The radula of *C. dentatum* (formula $\infty.4.1.4.\infty$) differs from that of *C. pulchrum* illustrated by Clench and

Turner (1960, pl. 3, fig. 3) by having four rather than five lateral teeth.

Calliostoma tenebrosum new species
(figures 27, 28)

Description: Shell medium-sized, attaining height of 13.6 mm, width of 11.5 mm, conical, nonumbilicate, finely sculptured. Protoconch slightly chipped, about 325 μm maximum diameter, 1 whorl. Teleoconch whorls 7.9, flat; first 3 whorls with low, rounded axial riblets and 2–4 strong, beaded spiral cords; axial riblets weakening on fourth whorl, becoming weak, irregular folds on subsequent whorls; spiral sculpture increasing by intercalation to 7 cords and 1 thread, of which abapical 3 cords forming periphery, beads on cords strong, rounded; periphery rather broadly rounded, adapical 2 peripheral cords strongest, subequal, separated by rather broad groove. Base very weakly convex, with 13 narrow, finely beaded spiral cords. Aperture subquadrate, moderately thickened within, lips thin, crenulate; columella very weakly concave, thickened, terminating in rounded tubercle. Shell ground color tan with spots of white and spots and axial streaks of dark brown.

Holotype: ANSP 300356, height 13.6 mm, width 11.5 mm.

Type locality: Off Potengi River, Natal, Estado Rio Grande do Norte, Brazil, depth unrecorded.

Distribution: This species is known only from the holotype, a hermit-crabbed shell, collected from a bottom of black mud in an unrecorded depth.

Remarks: *Calliostoma tenebrosum* is readily distinguished from other species of the *C. pulchrum* group by the relatively large, darkly colored shell that has the whorl periphery composed of three widely spaced spiral cords; the beads on the spiral cords are unusually large for this species group.

Calliostoma moseatellii new species
(figures 29, 30, 109)

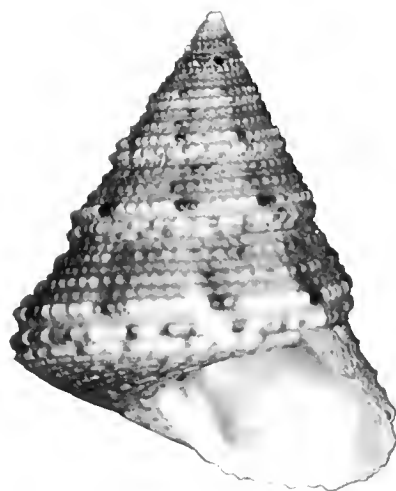
Calliostoma carcellesi: Rios, 1970:25, pl. 4 (partim); 1975:23, pl. 6, fig. 61 (partim). (Non *Calliostoma carcellesi* Clench & Aguayo, 1940).

Calliostoma (*Neocalliostoma*) *carcellesi*: Rios, 1985:22, pl. 10, fig. 88 (partim).

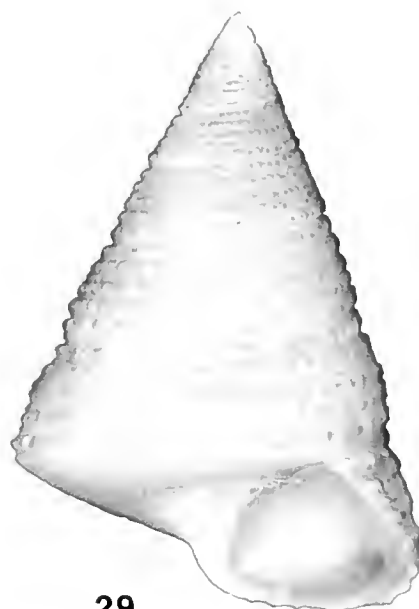
Description: Shell medium-sized, attaining height of 27.7 mm, width of 17.9 mm, conical, nonumbilicate, rather coarsely sculptured. Protoconch 375 μm maximum diameter, 1 whorl. Teleoconch whorls about 10, flat to weakly convex; first whorl with weak, rounded axial riblets and 2 strong, beaded spiral cords; axial riblets replaced on subsequent whorls by low, rounded, crowded plicae in interspaces between spiral cords, plicae strongest near suture and below peripheral cord; spiral sculpture increasing by intercalation to 5–8 cords and 4–9 threads, of which abaxial 2–3 strong cords and 2–3 weak



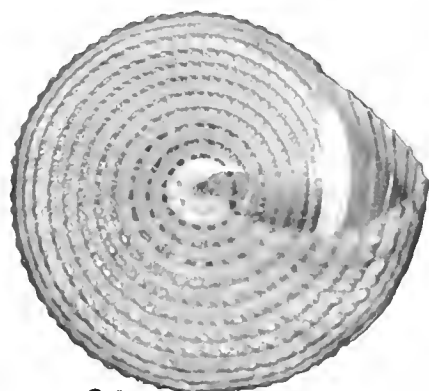
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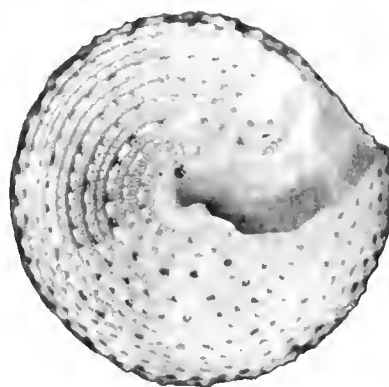
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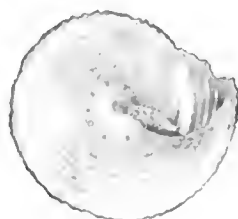
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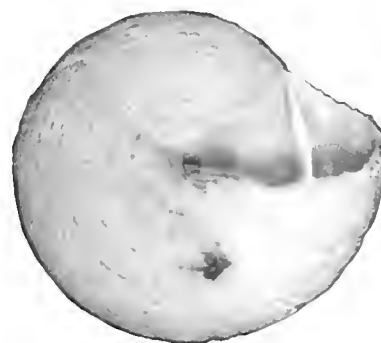
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31



32

cords or threads forming periphery, cords rather coarsely beaded, beads rounded, spirally elongate; periphery narrowly rounded. Base weakly convex, with 24–27 narrow, smooth to weakly beaded spiral cords and threads. Aperture subquadrate, lips thin, crenulate; columella short, straight, thickened. Shell ground color light yellowish or pinkish tan with greenish iridescence, diffuse patches of tan to reddish brown, and occasional discrete spots of light brown; 2–5 basal spiral cords with elongate spots of brown; protoconch and first 2 whorls lilac. Animal (in alcohol) white except brown sides of snout; cephalic tentacles long, broad, tapering abruptly near tip, ocular peduncles short (about 20% tentacle length), with large, black eye at tips; snout broad at base, tapering to rounded tip, tip with fringe of very small, short papillae; epipodium with 1 tentacle on left, 2 on right, left larger than right, neck lobes well developed, thin, semicircular, smooth.

Holotype: MORG 29.293, height 25.9 mm, width 17.7 mm.

Type locality: Off Ilha de Santana, Estado de Rio de Janeiro, Brazil, in approximately 50–80 m.

Paratypes: 1, USNM 860254; 1, MCZ 302591; 1, ANSP 389337; 1, FSBC 1 44075; 1, UF 189458; all from same lot as holotype.

Other material: 5, Coltro collection; from same lot as holotype.

Distribution: Numerous specimens of *C. moscatellii*, including live-collected specimens, have been obtained from depths of 50–200 m off Rio de Janeiro, Brazil, by shrimpers.

Remarks: Shells of *Calliostoma moscatellii* are very similar to those of *C. carcellesi* (figures 31, 32) but differ by being markedly narrower; by having a smaller protoconch (375 μ m vs. 400–425 μ m); by having fewer basal spiral cords, most of which are weakly but discretely beaded; by having more strongly spirally elongate beads on the supraproperipheral spiral cords; by having lilac apical whorls; and by having a distinct color pattern. *Calliostoma moscatellii* is also similar to *C. jucundum* but has narrower shells with more numerous, narrower spiral cords that bear much smaller, spirally elongate beads. The radula of *C. moscatellii* (formula $\infty.6.1.6.\infty$; figure 109) resembles that of *C. pulchrum* illustrated by Clench and Turner (1960:pl. 3, fig. 3) but has a broader rachidian tooth, and the cusps of the rachidian and lateral teeth are more finely denticulate.

This species is named for Sr. Renato Moscatelli, in recognition of his support of malacological publications in Brazil.

Calliostoma apicinum Dall, 1881
(figures 33, 34)

Calliostoma apicinum Dall, 1881:46; 1889b:162, pl. 24, figs. 3, 3a.—Pilsbry, 1890:379, pl. 60, figs. 1, 2.—Johnson, 1934:69.

Calliostoma (Calliostoma) apicinum: Dall, 1889a:366, pl. 24, figs. 3, 3a

Calliostoma roseolum: Clench & Turner, 1960:19, pl. 15, figs. 1, 2 (partim).—Abbott, 1974:43 (partim).—Quinn, 1979:26 (partim).—Sander & Lalli, 1982:table 4 (Non *Calliostoma roseolum* Dall, 1881).

Description: See Dall (1881:46).

Lectotype: (by implication of holotype; Clench & Turner, 1960): USNM 95013, height 7.7 mm, width 6.7 mm.

Type locality: Off Barbados, BLAKE station (number and coordinates unrecorded), in 183 m.

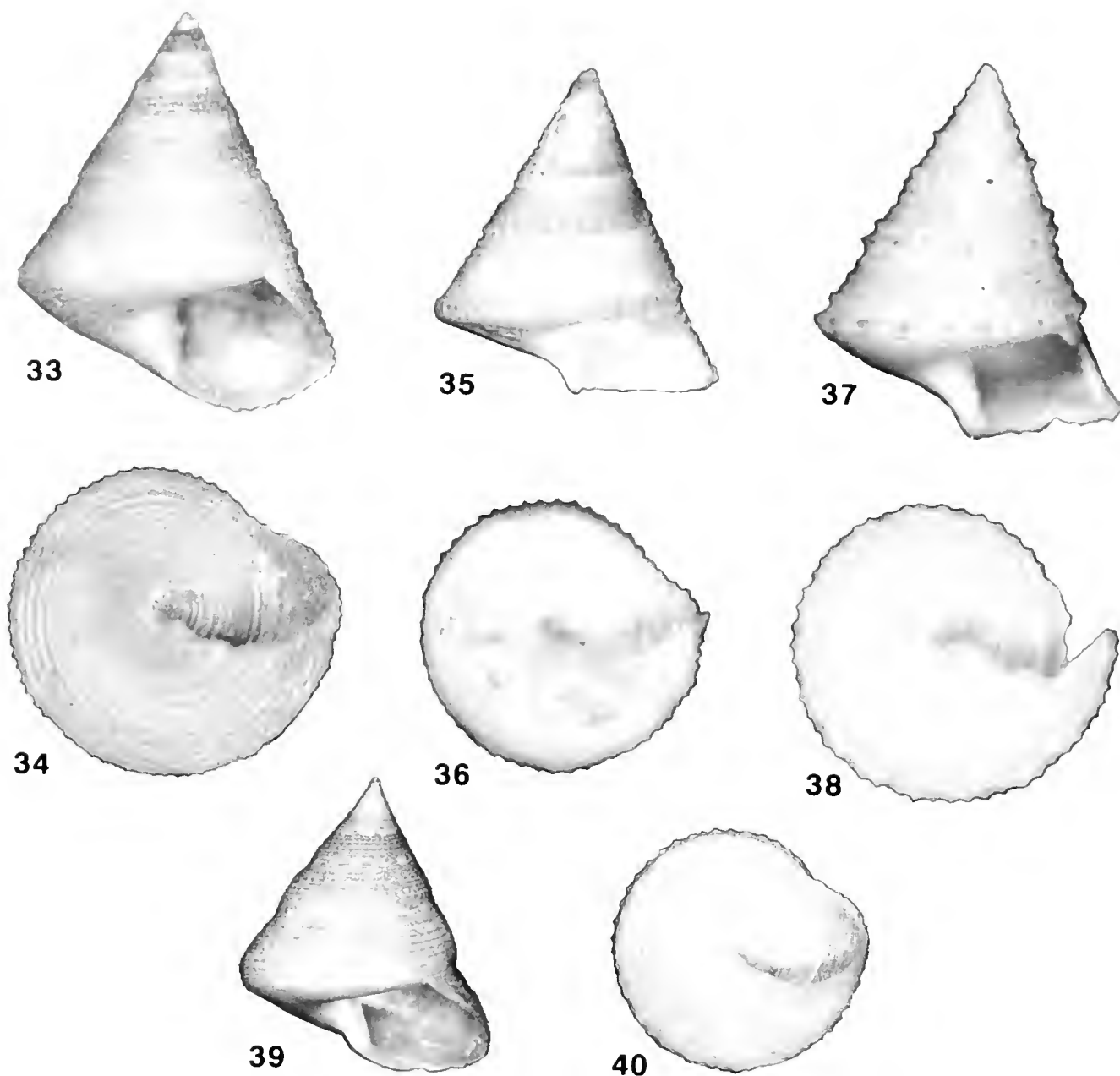
Paralectotypes: 1, USNM 95012; off Barbados, BLAKE Station 290, 13°11'54"N, 59°39'45"W, 134 m; 9 March 1879.—2, MCZ 7564; BLAKE station (number and coordinates unrecorded), 183 m.

Other material: 1, ANSP 353528; 1, FSBC 1 44077; off Hometown, Barbados, 175–225 m; ex F. Sander.—5, Sunderland collection; off St. James, Barbados, 100 m; dredge; ex F. Sander.—1, Sunderland collection; off St. James, Barbados, 152 m; 1988; ex F. Sander.—6, Sunderland collection; off St. James, Barbados, 175–225 m; ex F. Sander.—Several other specimens, all from Barbados, in private collections.

Distribution: This species is known only from off Barbados in depths of 100–225 m; I have only seen one live-collected specimen from a depth of 100 m.

Remarks: This species was synonymized with *Calliostoma roseolum* by Clench and Turner (1960), who thought that the shells described by Dall as *C. apicinum* were merely juveniles of *C. roseolum*. Shells of *C. apicinum*, however, are distinguished from those of *C. roseolum* by retaining flat-sided, peripherally subangulate whorls as adults (7+ whorls) rather than by having concave whorls with broadly rounded peripheries after the third or fourth whorl; by having a larger protoconch (360–375 μ m vs. 300–330 μ m) that has a purplish-brown tip; by having the apical two teleoconch whorls brown or purplish brown; by having more widely spaced, smooth

Figures 23, 24. *Calliostoma bermudense* new species, holotype, DMNH 187591; height 11.9 mm, width 8.9 mm. **Figures 25, 26.** *Calliostoma dentatum* new species, holotype, USNM 859358, height 5.7 mm, width 5.2 mm. **Figures 27, 28.** *Calliostoma tenebrosus* new species, holotype, ANSP 300356; height 13.6 mm, width 11.5 mm. **Figures 29, 30.** *Calliostoma moscatellii* new species, holotype, MORG 29.293; height 25.9 mm, width 17.7 mm. **Figures 31, 32.** *Calliostoma carcellesi* Clench & Aguayo, 1940, holotype, MCZ 104719; height 20.5 mm, width 17.5 mm



Figures 33, 34. *Calliostoma apicinum* Dall, 1881, specimen from off Barbados, FSBC 1 44077; height 10.0 mm, width 8.2 mm. Figures 35, 36. *Calliostoma debile* new species, holotype, USNM 860255; height 8.1 mm, width 7.0 mm. Figures 37, 38. *Calliostoma indiana* Dall, 1889, specimen from off Honduras, FSBC 1 44071; height 10.4 mm, width 9.0 mm. Figures 39, 40. *Calliostoma orion* Dall, 1881, specimen from JOHN ELLIOTT PILLSBURY Station P-425, UMMIL 30.3635; height 16.2 mm, width 14.4 mm.

or very weakly beaded spiral cords on the outer two-thirds of the base; by often having a chink-like umbilicus; and by having a shorter columella that often has a sub-conical, medial swelling. *Calliostoma apicinum* seems to be most closely related to the sympatric *C. debile* (see Remarks under the latter species for comparisons). Specimens that I can assign unequivocally to *C. apicinum* seem to come only from Barbados. Some other specimens with similar morphologies from the Bahama Islands (NICZ uncatalogued) and northwestern Cuba (NICZ 7566) are not here considered conspecific with the Barbados spec-

imens. A paralectotype of *C. apicinum* (MCZ 7565) from off Havana, Cuba, is definitely not this species; the specimen has a uniquely undulate peripheral spiral cord on several of the adapical teleoconch whorls and probably represents an undescribed species.

Calliostoma debile new species
(figures 35, 36)

Description: Shell small to medium-sized, attaining height of 10.3 mm, width of 8.7 mm, conical, nonum-

bilicate, finely sculptured. Protoconch 350–365 μm maximum diameter, 1 whorl. Teleoconch whorls 7.7, flat; first 2 whorls with low, rounded axial riblets and 2 strong, beaded spiral cords, abapical cord stronger on first 4 whorls, set with strong, conical beads; axial sculpture absent on subsequent whorls; spiral sculpture increasing by intercalation to 7–10 cords and 0–3 threads, of which abaxial 3, sometimes 2, cords forming periphery, supra-peripheral cords fine, sharp, finely beaded; periphery subcarinate, slightly projecting, peripheral cords stronger than supra-peripheral cords, set with conical beads. Base flat, with 10–14 narrow, flattened, smooth to weakly rugose spiral cords and 2–3 threads or weak cords near periphery. Aperture subquadrate, lips thin, weakly crenulate; columella straight, thickened. Shell ground color ivory, periphery light pinkish brown or with pale to bright spots of pinkish or yellowish brown or clear rose.

Holotype: USNM 860255, height 8.1 mm, width 7.0 mm.

Type locality: Off St. James, Barbados, in 175–225 m.

Paratype: 1, FSBC I 45776; off St. James, Barbados, 152 m; dredge; *ex* F. Sander.

Other material: 4, Sunderland collection; off St. James, Barbados, 152 m; 1985; dredge; *ex* F. Sander.—6, Sunderland collection; off St. James, Barbados, 175–225 m; dredge; *ex* F. Sander.

Distribution: *Calliostoma debile* is known only from empty shells collected off Barbados in 152–225 m.

Remarks: Shells of *Calliostoma debile* are most similar to those of the sympatric *C. apicinum* but differ by having a slightly smaller protoconch; by lacking the brown or purplish-brown apical whorls; by having a more projecting periphery, usually composed of three (sometimes two) close-set spiral cords; by usually having two to three spiral threads or weak cords between the circumbasal cord and the outermost strong basal spiral cord; by having distinct radial threads that finely bead the basal spiral cords; by having a less-thickened columella that lacks any indication of a medial swelling; and by lacking strong ridges within the aperture.

Calliostoma indiana Dall, 1889
(figures 37, 38)

Calliostoma (Eucasta) indiana Dall, 1889a:368, pl. 32, figs. 3, 5.—Abbott, 1974:46, fig. 333.

Calliostoma indiana: Clench & Turner, 1960:52, pl. 34, fig. 1.

Description: See Dall (1889a:368) and Clench and Turner (1960:52).

Holotype: USNM 214273, height 7.9 mm, width 6.9 mm.

Type locality: Off Grenada, Lesser Antilles, BLAKE Station 247, 12°05'25"N, 61°47'15"W, in 311 m.

Other material: 1, FSBC I 44071; off Honduras, CAPE

HATTERAS station, 15°32.36'N, 81°39.80'W, 50–85 m; 8 April 1987; rock dredge.

Distribution: This species is now known from two specimens, the holotype from Grenada and the CAPE HATTERAS specimen from off Honduras. Based on knowledge of the distributions of other species of *Calliostoma* (Clench & Turner, 1960, Quinn, herein, in press), I believe *C. indiana* probably inhabits deep fore-reef areas (50–150 m) of Central America and the Greater and Lesser Antilles.

Remarks: The new shell reported here is larger than the holotype (height 10.4 mm, width 9.0 mm), has five rather than four strong supra-peripheral cords, and has ten rather than seven basal spiral cords; otherwise the two shells are very similar. Based on shell characters, this species clearly belongs to the *C. pulchrum* species complex and is most similar to *C. echinatum*, *C. orion*, *C. sapidum*, and *C. cinctellum*.

Calliostoma orion Dall, 1889
(figures 39, 40)

Calliostoma orion Dall, 1889a:367, pl. 28, fig. 2; 1889b:162.—Pilsbry, 1890:383, pl. 48, fig. 18.—Johnson, 1934:70.—Clench & Turner, 1960:54, pl. 35, figs. 1, 2.—Quinn, 1981:151, figs. 1–13.

Description: See Dall (1889a:367) and Quinn (1981:151).

Holotype: USNM 214272, height 4.6 mm, width 4.3 mm.

Type locality: Off Havana, Cuba, BLAKE Station 62, in 146 m.

Other material: 2, FSBC I 31518; off western end of Isla de Roatán, Honduras, 19.8 m; 15 September 1982; SCUBA collection by W. C. Jaap.—1, Crnkovic collection; off western end of Isla de Roatán, Honduras, approximately 30 m; 1990; SCUBA collection by L. A. Crnkovic.—1, UMML 30.5688; off Isla de Roatán, Honduras, JOHN ELLIOTT PILLSBURY Station P-629, 15°58.2'N, 86°09.0'W, 40 m; 21 March 1968; 40-ft otter trawl.—1, UF 36324; Isla de Providencia, Colombia (off Nicaragua), "shallow water"; August 1971; C. R. Gilbert, collector.—1, UMML 30.3635; off Punta Manzanillo, Panamá, JOHN ELLIOTT PILLSBURY Station P-425, 9°38.9'N, 79°15.3'W, 70–64 m; 19 July 1968; 10-ft otter trawl.—3, Sunderland collection; off Barbados; *ex* F. Sander.

Distribution: *Calliostoma orion* is now known from almost the entire Caribbean coast of Central America, Cuba, the Bahama Islands, and Barbados.

Remarks: I discussed the ecology, shell and radular morphologies, and other distributional records in a previous paper (Quinn, 1981). The present specimens increase the maximum known size to 20.2 mm high, 17.1 mm wide; extend the maximum depth from which living specimens have been obtained from 43 m to 64–70 m;

and add new collection localities off Honduras, Nicaragua, and Panamá.

Calliostoma fernandezi Princz, 1978
(figures 41, 42)

Calliostoma fernandezi Princz, 1978:152–154, figs. 1, 2.

Description: Shell large, attaining height of 28.5 mm, width of 25.5 mm, conical, umbilicate, finely sculptured. Protoconch 350–375 μ m maximum diameter, 1 whorl. Teleoconch whorls more than 10, flat to concave; first 2 whorls flat-sided, with low, rounded axial riblets and 2–4 finely beaded spiral cords; axial sculpture absent on subsequent whorls; spiral cords increasing by intercalation to 17–22, of which abapical 3–4 cords forming periphery, all cords subequal and with well-defined, close-set, rounded beads; periphery narrowly rounded. Base flat to weakly convex, with 17–28 finely beaded spiral cords, those near periphery narrow, sharp, cords becoming broader and flatter adaxially, often splitting into 2 subequal cords; circumumbilical 1–2 cords strongest, tuberculate. Umbilicus funnel-shaped, 17%–24% maximum shell diameter, wall almost vertical, white. Aperture subquadrate, thickened within and with strong, sharp ridges, lips thin, crenulate; columella weakly sigmoid, thickened, terminating in blunt, rounded tubercle. Shell ground color cream to straw with irregular, diffuse patches of light brown above periphery; periphery with regular series of squarish, rose-brown to brown spots; interspaces of suprapерipheral spiral cords golden brown; base finely mottled with cream and yellow-brown.

Holotype: Collection of “Familia Fernández en Maracay, Estado Aragua, Venezuela” (Princz, 1978:152), height 14.7 mm, width 15.8 mm.

Type locality: “Grottos” at Las Cuevas Beach, Trinidad, depth not reported.

Other material: 1, UMML 30.7162; off Península de la Guajira, Colombia, JOHN ELLIOTT PILLSBURY Station P-769, 12°31.0'N, 71°41.0'W, 143–146 m; 28 July 1968; 10-ft otter trawl.—1, UMML 30.6424; off Península de Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-709, 11°08.8'N, 62°46.1'W, 46 m; 19 July 1968; 10-ft otter trawl.—1, UMML 30.6454; off Península de Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-708, 11°24.7'N, 62°40.5'W, 69–73 m; 19 July 1968; 10-ft otter trawl.—1, UMML 30.6373; off Península de Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-707, 11°21'N, 62°21'W, 75 m; 19 July 1968; 10-ft otter trawl.—1, UMML 30.6373; off Península de Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-705, 10°45'N, 62°00'W, 77–86 m; 18 July 1968; 10-ft otter trawl.—2, MCZ 273512; Georgetown, Guyana, CHAIN Cruise 35, Station 35+36, 8°10.5'–8°10.0'N, 57°48'W, 97–110 m; 28 April 1963.—2, USNM 866503; 1, FSBC 1 44072; 1, UF 189459; 5, UMML 30.5840; off Pointe Isère, French Guiana, JOHN ELLIOTT PILLSBURY Station P-650, 6°07'N, 52°19'W, 84–91 m; 8 July 1968; 10-ft otter trawl.

Distribution: *Calliostoma fernandezi* occurs from Suriname northward and westward to off Cabo de la Vela, Colombia, in depths of about 45–245 m; living specimens have been collected from depths of 84–146 m.

Remarks: Although the description presented by Princz (1978) is incomplete, the specimens recorded here seem to be referable to *Calliostoma fernandezi*. The shells of this species are very similar to those of *C. scalenum* but differ by having a larger protoconch (375 μ m vs. 320–325 μ m); by having fewer, stronger, more evenly sized spiral cords; by having stronger, more closely spaced, and more symmetrical beading; by having an umbilical wall that is almost vertical rather than sloping steeply inward; and by having a different, lighter color pattern. The spiral cords at the periphery and on the base of shells of *C. fernandezi* tend to increase in number by fission of existing cords rather than by intercalation of new cords; this tendency is rare among species of *Calliostoma* that I have examined.

Data obtained from the original field data sheets indicate that *C. fernandezi* occurs on shell-hash and coral-rubble bottoms, often in association with sponges and octocorals.

Calliostoma scalenum new species
(figures 43, 44, 110, 111)

Description: Shell large to very large, attaining height of 40.6 mm, width of 34.2 mm, conical, umbilicate, finely sculptured. Protoconch 320–325 μ m maximum diameter, 1 whorl. Teleoconch whorls about 10, first 4–5 whorls flat-sided, subsequent whorls weakly to strongly concave; first 3 whorls with low, rounded axial riblets and 2–6 finely beaded spiral cords; axial sculpture absent on subsequent whorls; spiral cords increasing by intercalation to 25–30, of which abapical 8–12 cords forming periphery, alternating in size, finely beaded, beads close-set, rounded, conical; periphery narrowly rounded. Base flat to weakly convex, with as many as 42 narrow, weakly beaded spiral cords, those on abaxial half alternating in size, those on adaxial half subequal except 2–3 stronger, tuberculate circumumbilical cords. Umbilicus funnel-shaped, 14%–23% maximum shell diameter, wall smooth, white, often with yellow-brown flush. Aperture subquadrate, thickened within and with strong ridges, lips thin, crenulate; columella sigmoid, thickened, terminating in blunt, rounded tubercle. Shell ground color light chestnut to red-brown with irregular, diffuse axial flammules of darker ground color and white; light and dark flammules more distinct and closely spaced on periphery. Animal (in alcohol) white; foot with numerous, scattered, small, opaque, white spots; cephalic tentacles long, tapered, bases with short ocular peduncles bearing small, black eye at tips; epipodium with 4 pairs of tentacles, neck lobes well-developed, thin, semicircular, smooth-edged.

Holotype: USNM 859356, height 31.5 mm, width 25.9 mm.

Type locality: Stetson Bank, southeast of Galveston, Texas, 28°09'54"N, 94°18'00"W, in 21–27 m.

Paratypes: 2, HMNS 15022; 2, USNM 859357; 1, MCZ 297051; 1, ANSP 367152; 1, AMNH 225980; 1, LACM 2292; 1, UF 110222; 2, FSBC 132315; 34, HMNS 15850; all from same lot as holotype.—3, ANSP 338470; off Freeport, Texas, NW Gulf Survey station, 28°10'N, 94°55'W, 51 m; dredge; A. Kight, collector.

Other material: More than 200 lots listed by Quinn (in press).

Distribution: *Calliostoma scalenum* inhabits offshore waters on calcareous substrates from North Carolina southward through the Florida Keys and throughout the Gulf of Mexico in depths of 25–80 m.

Remarks: Shells of *Calliostoma scalenum* have been identified previously as *C. jujubinum* without exception (see Quinn, in press, for complete synonymy). *Calliostoma scalenum* differs from *C. jujubinum* by having shells that are larger and more narrowly conical; that have a slightly larger protoconch (320–325 μ m vs. 315 μ m); that lack fine, collabral threads after the fourth or fifth whorls; that have two rather than three distinct sizes of spiral cords with discrete, symmetrical rather than spirally elongate beads; that have a greater number of spiral cords, particularly on the base (35–42 vs. 25–30 total); and that lack very dark-colored apical whorls. Shells of *C. scalenum* are also similar to those of *C. tampaense* but differ by having straight-sided apical whorls that lack a strong, sharply beaded peripheral carina; by having finer, more numerous, and more finely beaded spiral cords; and by being proportionately much narrower. Both *C. jujubinum* and *C. tampaense* are also shallow-water species, neither species occurring alive in depths exceeding 11 m (Quinn, in press). The radula of *C. scalenum* (formula $\infty.6.1.6.\infty$; figures 110, 111) is very similar to that of *C. tampaense* illustrated by Clench and Turner (1960:pl. 5, fig. 2, as *C. jujubinum*) and *C. vinosum* (figure 114 herein) in having six pairs of lateral teeth, of which the outer two pairs lack cusps. Radulae of *C. jujubinum* (figure 112) and *C. cubense* (figure 113) are also very similar in morphology but differ in having only five pairs of lateral teeth. One character common to all of these radulae is that the cusps of the inner lateral teeth arise from the outer corner of the tooth bases; this characteristic has not been explicitly noted before and is not clear in any of the previously published line drawings (Clench & Turner, 1960:pl. 5, figs. 1, 2; Calvo, 1987: fig. 26).

Calliostoma cubense new species
(figures 45, 46, 113)

Description: Shell medium-sized, attaining height of 16.6 mm, width of 14.3 mm, conical, umbilicate, rather coarsely sculptured. Protoconch about 350 μ m maximum diameter, 1 whorl. Teleoconch whorls 7–8, flat to weakly concave; first 2–3 whorls with low, sharp axial riblets and

2–4 strong, beaded spiral cords; axial riblets replaced by low, crowded, rounded axial threads in interspaces between primary spiral cords; spiral cords increasing by intercalation to 6–12, of which abapical 1–2 beaded cords and broad, smooth cord forming periphery, usually alternating in size, primary cords strongly beaded, secondary cords smooth or finely beaded by axial threads; periphery narrowly rounded, smooth peripheral cord often dissected by 1 (rarely 3–5) fine, spiral stria. Base flat to weakly convex, with 10–13 narrow, smooth or weakly beaded spiral cords. Umbilicus funnel-shaped, 18%–21% maximum shell diameter, wall white. Aperture subquadrate, thickened within and with strong ridges, lips thin, crenulate; columella sigmoid, thickened, terminating in moderately strong, rounded denticle. Shell ground color tan to pinkish brown with numerous white dots, principally on individual beads of primary spiral cords but broader on periphery; interspaces between spiral sculpture golden brown, usually at periphery and on base, occasionally above periphery. Animal (reconstituted in trisodium phosphate) uniformly tan; cephalic tentacles long, slender, gradually tapering; eyestalks short (about 10%–15% tentacle length), stout, with large black eye at tips; snout longer than broad, with fringe of fine, short papillae; epipodium with 3 pairs of long tentacles; neck lobes well-developed, left lobe finely digitate, right lobe smooth-edged.

Holotype: ANSP 196933, height 14.7 mm, width 13.7 mm.

Type locality: Off Pini Pini, Cárdenas Bay, Matanzas, Cuba, in 11 m.

Paratypes: 4, USNM 438265; TOMÁS BARRERA Expedition Station 224, Cabo San Antonio, Pinar del Río, Cuba.—12, ANSP 196926; off Cárdenas Bay, Matanzas, Cuba, 11 m; 11 February 1954; V. Conde, collector.—9, ANSP 357161; 2, FSBC 132405; from same lot as holotype.—2, MCZ 204705; Península de Hicacos, Matanzas, Cuba; 1940; V. Conde, collector.—4, MCZ 216120; Cayo Fragoso, Villa Clara, Cuba; R. Humes, collector.—1, MCZ 235536; off Cayo Fragoso, Villa Clara, Cuba; R. T. Abbott, collector.—5, MCZ 129623; Cayo Francés, Villa Clara, Cuba; ex P. J. Bermudez collection.—3, ANSP 216122; Caibarién, Villa Clara, Cuba; R. Humes, collector.

Distribution: This species seems to be restricted to the northern coast of Cuba; live-collected specimens were obtained from off Pini Pini in 11 m.

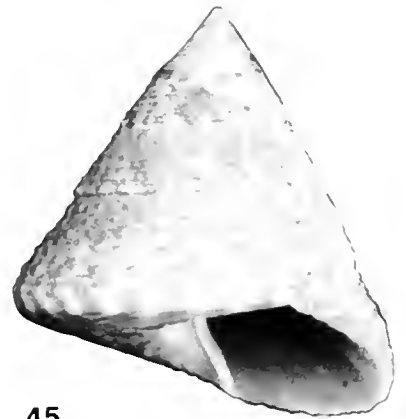
Remarks: Shells of *Calliostoma cubense* most resemble those of *C. adelae* in shape and size and in having rather coarse sculpture relative to other species of the *C. jujubinum* species complex. Shells of *C. cubense* differ from those of *C. adelae* by having more numerous, unequally sized spiral cords both above and below the periphery; by having the basal spiral cords closely spaced, separated by narrow, V-shaped grooves, rather than widely spaced and separated by broad, flat-bottomed



41



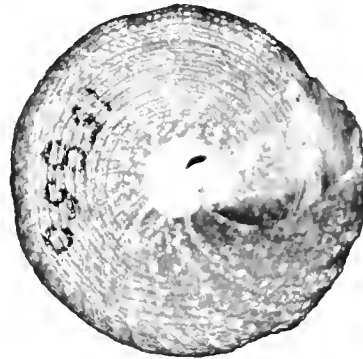
43



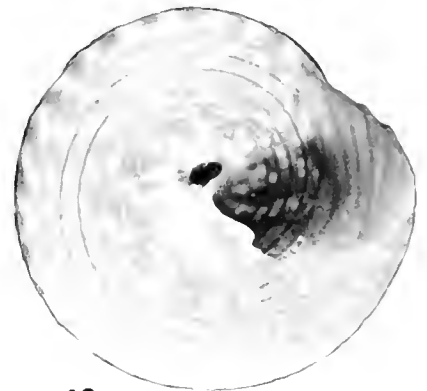
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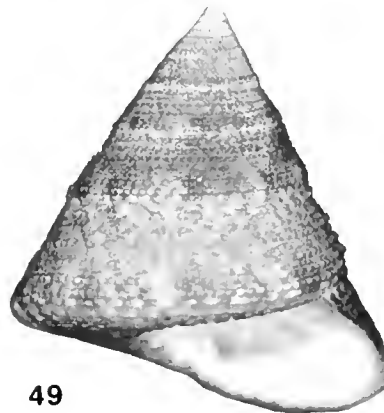
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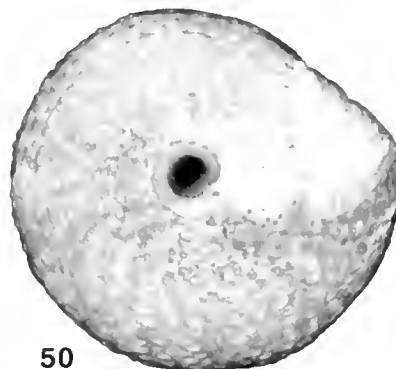
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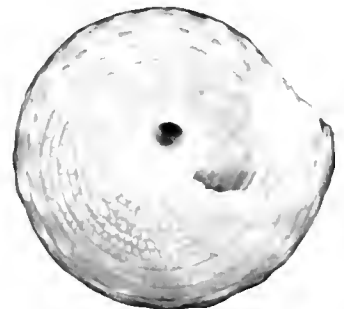
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52

grooves; by having distinct, fine collabral threads between the supraparipheral spiral cords; and by having a rather broad and smooth rather than narrow and strongly beaded peripheral cord. The shells of *C. cubense* from the TOMÁS BARRERA Expedition (USNM 438265) are apparently those that Henderson (1916:185) recognized as "an apparently new *Calliostoma*" from dredgings off Cabo Cajón (near Cabo San Antonio) on a bottom of coral sand with patches of seagrass and sponge, the area swept by strong currents.

The intestine of one specimen (*ex* FSBC 1 32405) was packed with amorphous organic material, hydroid stalks, and several different forms of foraminiferans.

Calliostoma purpureum new species
(figures 47–50)

Description: Shell medium-sized, attaining height of 23.9 mm, width of 20.2 mm, conical, umbilicate, rather coarsely sculptured. Protoconch unknown. Teleoconch whorls about 9, flat to weakly convex; first 1–2 whorls worn on all specimens but apparently with axial riblets and 2–4 spiral cords; axial sculpture absent on subsequent whorls; spiral sculpture increasing by intercalation to 8–14 cords and 1–8 fine threads, of which abapical 3–5 cords forming periphery; periphery broadly rounded. Base flat to weakly convex, with 13–18 coarsely beaded spiral cords. Umbilicus funnel-shaped, 18%–26% maximum shell diameter, wall white to intense violet. Aperture subquadrate, thickened within and with strong, sharp ridges, lips thin, crenulate; columella weakly sigmoid, thickened, often with 1–3 small, sharp denticles or ridges on lower third, terminating in strong, rounded tubercle. Shell ground color tan to reddish brown, mottled with cream to yellowish brown.

Holotype: USNM 860247, height 21.1 mm, width 19.6 mm.

Type locality: Off Cabo de la Vela, Colombia, in 61–91 m.

Paratypes: 3, USNM 860248; 1, FSBC 1 44074; from same lot as holotype.

Other material: 5, Deynzer collection; from same lot as holotype.—1, UMML 30.7204; off Cabo de la Vela, Colombia, JOHN ELLIOTT PILLSBURY Station P-773, 12°17.0'N, 72°15.0'W, 60–64 m; 29 July 1968; 10-ft otter trawl.—3 broken, FSBC 1 32742; about 5 km north of La Guardia, Isla de Margarita, Venezuela, beach drift; 19 November 1987; W. G. & C. B. Lyons, collectors.—15 broken, FSBC 1 32747; 6 km north of La Guardia,

Isla de Margarita, Venezuela, beach drift; 18 November 1987; W. G. & C. B. Lyons, collectors.—1, UMML 30.7269; off Galera Point, Trinidad, JOHN ELLIOTT PILLSBURY Station P-840, 10°40.5'N, 60°37.5'W, 33–37 m; 1 July 1969; 10-ft otter trawl.

Distribution: *Calliostoma purpureum* is known from off northeastern Colombia, Isla de Margarita, Venezuela, and Trinidad; most specimens have been collected from 33–91 m, but broken shells are also known from beach drift.

Remarks: Shells of *Calliostoma purpureum* are very similar to those of *C. jujubinum* but differ by lacking collabral threads between the spiral cords, by having the spiral cords narrower and more finely beaded, and by having the umbilical wall almost vertical rather than strongly sloped. Most specimens of *C. purpureum* have one or more small, sharp denticles on the columella, whereas specimens of *C. jujubinum* very rarely have only a single denticle; I know of no other species that has a denticulate columella. Additionally, whereas specimens of *C. jujubinum* may have the umbilical wall flushed with pinkish brown, I have never seen any specimen of that or any other species of western Atlantic *Calliostoma* with the violet color or the intensity of any other color displayed on the umbilical wall of specimens of *C. purpureum* except the red-brown in *C. brunneum* and *C. barbouri*. Shells of *C. purpureum* may have been reported from Curaçao by de Jong and Coomans (1988) as *C. tampaense*.

Almost all of the specimens collected at Isla de Margarita consisted of only the last one to three whorls; because the damage to these shells is almost identical to that illustrated by Vermeij (1978: fig. 2.10), this damage may have been the result of predation by xanthid crabs. This species has been collected principally in areas with large concentrations of sponges and was probably the species from Islas Los Roques, Venezuela, that Work (1969) observed eating an encrusting sponge.

Calliostoma fucosum new species
(figures 51, 52)

Description: Shell medium-sized, attaining height of 12.8 mm, width of 12.6 mm, conicoturbinata, umbilicate, rather coarsely sculptured. Protoconch eroded. Teleoconch whorls about 7, weakly concave; first whorl eroded, next whorl with 3 strong, strongly beaded spiral cords; spiral cords increasing by intercalation to 7, of which abapical 2 cords forming periphery; periphery broadly rounded, adapical peripheral cord beaded, abapical pe-

Figures 41, 42. *Calliostoma fernandesi* Princz, 1978, specimen from JOHN ELLIOTT PILLSBURY Station P-650, UMML 30.5840; height 21.5 mm, width 19.3 mm. **Figures 43, 44.** *Calliostoma scalenum* new species, holotype from Stetson Bank, SE of Galveston, Texas, USNM 859356; height 31.5 mm, width 25.9 mm. **Figures 45, 46.** *Calliostoma cubense* new species, holotype from Pini Pini, Cuba, ANSP 196933; height 14.7 mm, width 13.7 mm. **Figures 47–50.** *Calliostoma purpureum* new species. **47, 48.** Holotype, USNM 860247; height 21.1 mm, width 19.6 mm. **49, 50.** Paratype, USNM 860248; height 15.8 mm, width 15.4 mm. **Figures 51, 52.** *Calliostoma fucosum* new species, holotype, USNM 860259; height 12.8 mm, width 12.6 mm.

ripheral cord smooth with shallow medial stria. Base weakly convex, with 9 broad, coarsely beaded and 2 narrow, smooth spiral cords; circumumbilical cord strongest and most strongly beaded. Umbilicus 20% maximum shell diameter, wall white with faint flush of pink. Aperture subquadrate, lips thin, weakly crenulate; columnella weakly sigmoid, somewhat thickened, terminating in sharp denticle. Shell ground color predominantly orange-brown with spots and flammules of white and darker orange-brown.

Holotype: USNM 860259, height 12.8 mm, width 12.6 mm.

Type locality: Off Cabo de la Vela, Colombia, JOHN ELLIOTT PILLSBURY Station P-774, 11°56.5'N, 72°17.9'W, in 5–9 m.

Distribution: This species is only known from the holotype shell.

Remarks: The holotype of *Calliostoma fucosum* resembles a small *C. euglyptum*, but the shell is umbilicate, proportionately broader, has stronger and coarser sculpture, and has a much brighter color pattern.

The specimen of *C. fucosum* was trawled in shallow water from a bottom composed principally of calcareous red algae (UMML, unpublished).

Calliostoma vinosum new species
(figures 53–56, 114)

Calliostoma (*Elmerlinia*) *bullisi*: Rios, 1970:24, pl. 5. (Non *Calliostoma bullisi* Clench & Turner, 1960).

Calliostoma barbouri: Rios, 1975:23, pl. 5, fig. 60; 1985:22, pl. 10, fig. 87. (Non *Calliostoma barbouri* Clench & Aguayo, 1946).

Calliostoma javanicum: Leal, 1991:45, 353 (partim). (Non *Trochus javanicum* Lamarek, 1822).

Description: Shell medium-sized, attaining height of 19.8 mm, width of 21.3 mm, conical, umbilicate, finely sculptured. Protoconch 325–350 μ m maximum diameter, 1 whorl. Teleoconch whorls 8, flat to weakly convex; first whorl initially with 2 strong spiral cords and low, rounded axial riblets; axial sculpture absent after first one-third whorl; spiral sculpture increasing by intercalation to 9–15 beaded cords and 0–6 smooth to finely beaded threads, of which abapical 2 cords forming periphery, beads rounded; surface of first 4–5 whorls microscopically frosted; periphery narrow, subcarinate, abapical peripheral cord often with shallow, median groove. Base flat to weakly concave, with 12–14 narrow, finely beaded spiral cords and 0–3 spiral threads. Umbilicus funnel-shaped, 18%–22% maximum shell diameter, wall smooth, white or flushed with yellow. Aperture subquadrate, lips thin, crenulate; columnella weakly sigmoid, weakly thickened, terminating in sharp denticle. Shell ground color deep red-brown with crescentic streaks of yellow-brown above periphery; base golden brown with 6–9 spiral lines of red-brown. Animal (in alcohol): foot red-brown with large, white papillae; mantle with narrow band of white and

red-brown spots at edge behind which is series of dark brown spots extending posteriorly as gradually fading streaks; cephalic tentacles red-brown with darker median stripe, white near base, left tentacle stout, about length of snout, right tentacle longer and more slender; snout long, broad, mottled red-brown and white, with anterior fringe of long papillae; epipodium with 4 pairs of red-brown tentacles, neck lobes well-developed, semicircular, left lobe smooth, right lobe finely fringed.

Holotype: MORC 29.294, height 13.5 mm, width 15.3 mm.

Type locality: Off Guarapari, Estado de Espirito Santo, Brazil, in 18–22 m.

Paratypes: 1, USNM 860256; 1, FSBC 1 44067; both from same lot as holotype.—1, MORC 15.043; off Cabo Orange, Estado de Amapá, Brazil, ALMIRANTE SALDANHA Station 2029, 103 m; 30 November 1968.

Other material: 1, MNHN uncatalogued; MARION-DUFRESNE Cruise MD-55, Station DC-40, 20°40'S, 34°41'W, 60 m; 17 May 1987; dredge.—2, MNHN uncatalogued; MARION-DUFRESNE Cruise MD-55, Station DC-47, 20°42'S, 32°13'W, 94–105 m; 19 May 1987; dredge.—2, MNHN uncatalogued; MARION-DUFRESNE Cruise MD-55, Station DC-42, 20°55'S, 34°01'W, 60 m; 17 May 1987; dredge.—7, MNHN uncatalogued; MARION-DUFRESNE Cruise MD-55, Station DC-15, 21°37'S, 40°18'W, 37 m; 11 May 1987; dredge.

Distribution: *Calliostoma vinosum* is known in north-eastern Brazil from the Amazon River to just north of Rio de Janeiro, in 18–105 m.

Remarks: Shells of *Calliostoma vinosum* are most similar to those of *C. barbouri* in shape, size, and color but differ by having a somewhat smaller protoconch (325–350 μ m vs. 350–400 μ m); by having flat-sided rather than convex whorls; by having fewer, stronger, more coarsely beaded spiral cords, particularly on the base; by having axial riblets that disappear early on the first whorl rather than persisting onto the second whorl; by lacking collabral threads between the primary spiral cords; and by having the first 4–5 whorls more distinctly frosted.

Most of the specimens examined for this study were trawled from bottoms on which bryozoans and coralline algae were abundant (J. & M. Coltro, personal communication; Leal, 1991).

Calliostoma alternum new species
(figures 57, 58)

Description: Shell medium-sized, attaining height of 15.6 mm, width of 13.9 mm, conical, umbilicate, finely sculptured. Protoconch about 350 μ m maximum diameter, 1 whorl. Teleoconch whorls about 8.5, flat; first 4 whorls with low, rounded axial riblets and 2–7 beaded spiral cords; axial sculpture reduced to fine collabral threads or absent on subsequent whorls; spiral sculpture

increasing by intercalation to 7–11 beaded cords and 5–6 threads, of which abapical 3 cords forming periphery; periphery narrowly rounded. Base weakly convex, with 17 narrow, finely beaded spiral cords. Umbilicus 22%–24% maximum shell diameter, wall almost vertical, white. Aperture subquadrate, lips thin, weakly crenulate; columella weakly sigmoid, rather thin, terminating in small, rounded denticle. Shell ground color uniformly ivory or with very faint peripheral light brown maculations.

Holotype: USNM 860257, height 15.6 mm, width 13.9 mm.

Type locality: Northeast of Caracas, Venezuela, JOHN ELLIOTT PILLSBURY Station P-737, 10°44.0'N, 66°07.0'W, in 60–73 m.

Paratypes: 1, UMML 30.8374; off Península de la Guajira, Colombia, JOHN ELLIOTT PILLSBURY Station P-769, 12°31.0'N, 71°41.0'W, 143–146 m; 28 July 1968; 10-ft otter trawl.—1, UMML 30.6155; off Suriname, JOHN ELLIOTT PILLSBURY Station P-684, 7°19.0'N, 56°51.0'W, 55–59 m; 14 July 1968; 10-ft otter trawl.

Distribution: Shells of this species are known from northeastern Colombia, Venezuela, and Suriname, in 55–146 m.

Remarks: Shells of *Calliostoma alternum* are most similar to those of *C. aulicum* but differ by being evenly conical rather than eoeloonoid; by having a more rounded, less strongly projecting periphery; by having fewer, stronger, more coarsely beaded spiral cords, most of which are separated by a fine spiral thread; by having axial riblets that persist on the first four whorls rather than only on the first two; and by having the abapical of the two primary spiral cords remaining conspicuously strong on first five whorls.

The specimens of *C. alternum* were collected on bottoms composed of carbonate rock covered by calcareous algae and sponges (UMML, unpublished).

Calliostoma aulicum new species
(figures 59–62)

Description: Shell medium-sized, attaining height of 15.9 mm, width of 16.1 mm, conical, umbilicate, finely sculptured. Protoconch about 350 μ m maximum diameter, 1 whorl. Teleoconch whorls 7.3, weakly concave; first two whorls with low, rounded axial riblets and 2–3 beaded spiral cords; axial sculpture absent after second whorl; spiral cords strongly beaded, increasing by intercalation to 10–12, of which abapical 3 strongest cords forming periphery on last whorl, beads rounded; periphery narrowly rounded. Base flat to weakly convex, with 17–19 narrow, finely beaded spiral cords. Umbilicus funnel-shaped, 17%–20% maximum shell diameter, wall white. Aperture subquadrate, thickened and strongly ridged within, lips thin, crenulate; columella weakly sigmoid, thickened, terminating in narrow denticle. Shell ground color ivory with few, faint patches of golden brown.

Holotype: USNM 860258, height 15.9 mm, width 16.1 mm.

Type locality: Off Colón, Panamá, JOHN ELLIOTT PILLSBURY Station P-451, 9°22.0'N, 79°56.0'W, in approximately 12 m.

Paratype: 1, UMML 30.8375; off Suriname, JOHN ELLIOTT PILLSBURY Station P-669, 6°39.0'N, 55°15.5'W, 33 m; 10 July 1968; 10-ft otter trawl.

Other material: 1 fragment, UMML 30.7238; off Orinoco River, Venezuela, JOHN ELLIOTT PILLSBURY Station P-835, 9°36.0'N, 60°10.0'W, 48 m; 30 June 1968; 10-ft otter trawl.—1 fragment, UMML 30.7306; off Galera Point, Trinidad, JOHN ELLIOTT PILLSBURY Station P-840, 10°40.5'N, 60°37.5'W, 33–37 m; 1 July 1968; 10-ft otter trawl.

Distribution: *Calliostoma aulicum* is known from off Panamá and eastern Venezuela in 12–48 m.

Remarks: Shells of this species are very similar to those of *Calliostoma tampaense* but differ by having a slightly larger protoconch (350 μ m vs. 325 μ m); by having a more broadly rounded, more strongly projecting periphery; by being much thicker; by having more strongly beaded basal spiral cords; and by lacking a distinct color pattern. If the holotype of *C. aulicum* represents the size of a fully grown adult, as the thickened and ridged aperture seems to indicate, then *C. aulicum* is much smaller than *C. tampaense*, shells of which attain a height of about 30 mm (Quinn, in press).

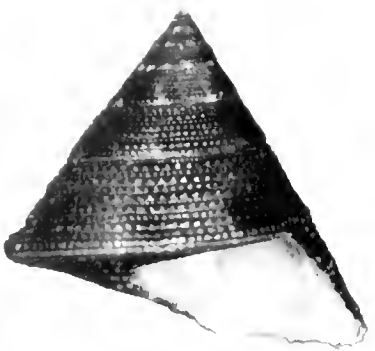
Calliostoma hirtum new species
(figures 63, 64)

Description: Shell medium-sized, attaining height of 17.9 mm, width of 19.8 mm, conical, umbilicate, finely sculptured. Protoconch missing. Teleoconch whorls about 7, flat to weakly concave; first remaining whorl worn smooth; next whorl with 4 beaded spiral cords, cords increasing to 13, of which abapical 2 cords forming periphery on last whorl, beads conical; periphery carinate, adapical peripheral cord stronger than abapical peripheral cord. Base weakly concave to weakly convex, with 17–18 narrow, weakly beaded spiral cords. Umbilicus funnel-shaped, 20% maximum shell diameter, wall almost vertical, white or yellow-brown. Aperture subquadrate, lips thin, crenulate; columella weakly sigmoid, thin. Shell ground color light yellow-brown with diffuse flammules of cream and light brown; interspaces between several spiral cords golden brown.

Holotype: USNM 860260, height 17.9 mm, width 19.8 mm.

Type locality: Off Navidad Bank, northeast of the Dominican Republic, JOHN ELLIOTT PILLSBURY Station P-1160, 20°01'N, 68°51'W, in 521 m.

Paratype: 1, UMML 30.8371; from same lot as holotype.



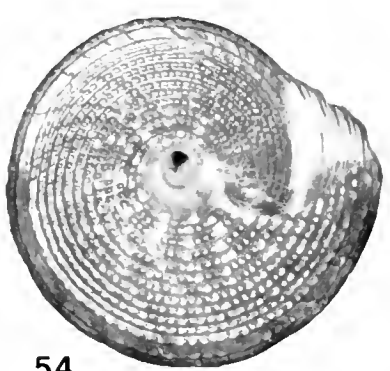
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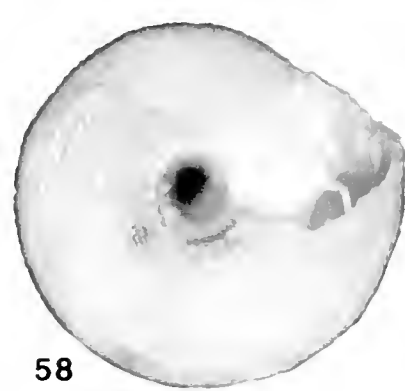
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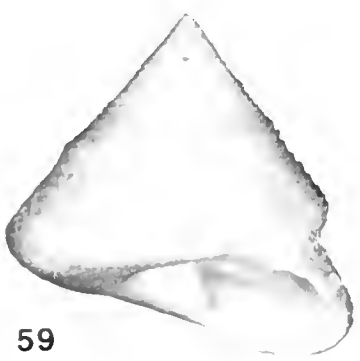
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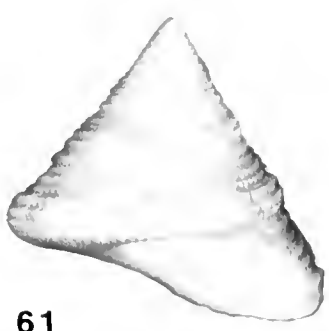
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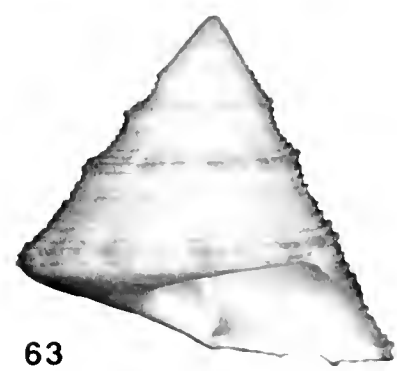
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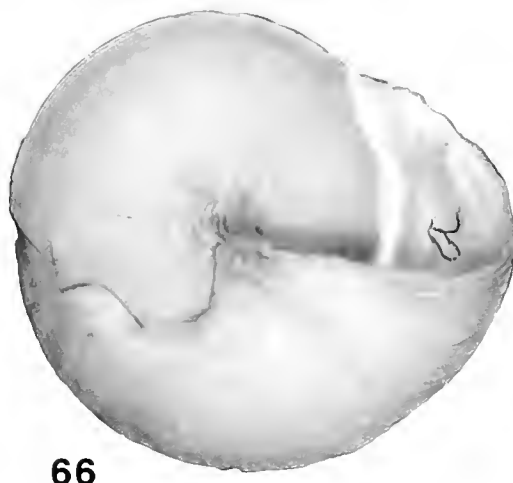
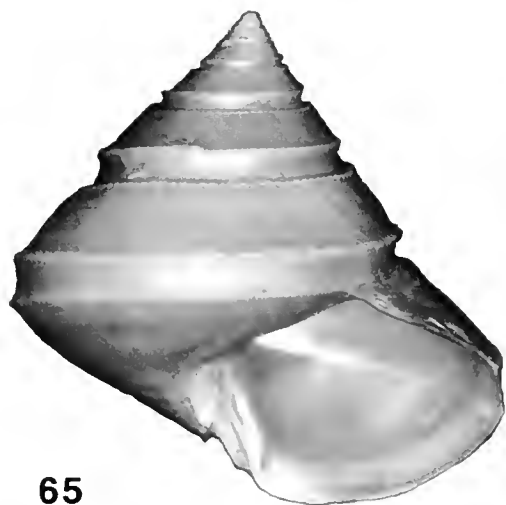
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Figures 65, 66. *Calliostoma atlantis* Clench & Aguayo, 1940, holotype, MCZ 135164; height 32.7 mm, width 33.6 mm.

Distribution: This species is known only from the type locality.

Remarks: The shells of *Calliostoma hirtum* are most similar to those of *C. javanicum* but differ by having a stronger, more sharply beaded peripheral cord; by lacking axial sculpture in the interspaces between the spiral cords; and by having more numerous, sharper spiral cords, particularly on the outer part of the base.

Calliostoma atlantis Clench & Aguayo, 1940 (figures 65, 66)

Calliostoma (*Calliostoma*) *atlantis* Clench & Aguayo, 1940, St, pl. 13, fig. 4

Calliostoma atlantis: Clench & Turner, 1960:62, pl. 44; Harasewych, 1989:27, pl. 17.

Calliostoma (*Kombologion*) *atlantis*: Abbott, 1974:45.

Description: See Clench and Aguayo (1940:81) and Clench and Turner (1960:62).

Holotype: MCZ 135164, height 32.7 mm, width 33.6 mm.

Type locality: Northwest of Mariel, Cuba, ATLANTIS Station 3306, 23°04'30"N, 82°37'00"W, in 604 m.

Other material: 1, USNM 869000; off Great Inagua Island, Bahama Islands, JOHNSON-SEA-LINK I Station JSL-I-2323, 21°01'45"N, 74°43'48"W, 628 m; 15 October 1988.

Distribution: The specimen of this species reported here is only the second collected and extends the range from

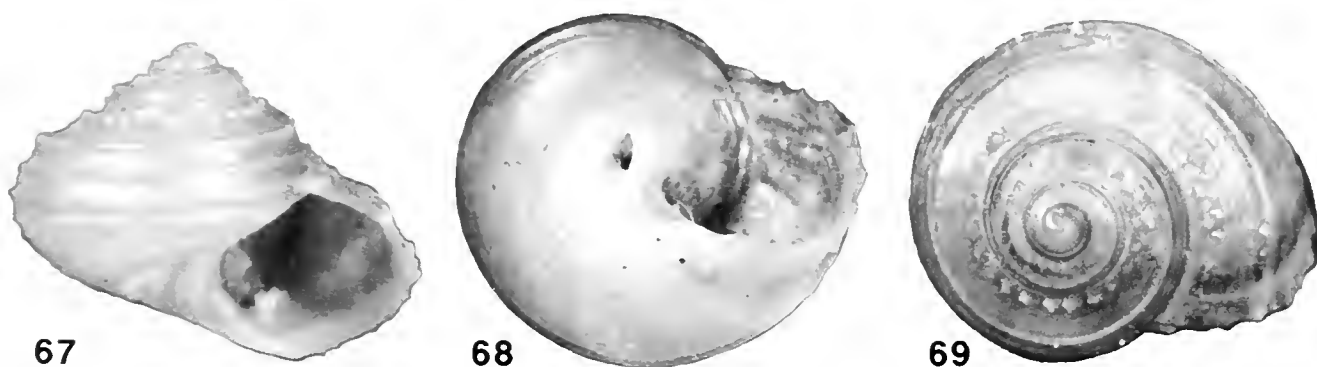
northwestern Cuba to off Great Inagua Island northeast of the eastern tip of Cuba. This specimen was collected by M. G. Harasewych, using the submersible JOHNSON-SEA-LINK I from a large boulder in 628 m, a depth very similar to that from which the holotype was collected (604 m). The animal was reported to be bright red (Harasewych, 1989:27).

Remarks: Based on shell characters, *Calliostoma atlantis*, *C. torrei*, *C. dnopherum*, and the new species *C. rugosum*, *C. atlantoides*, *C. rota*, and *C. coronatum* form a distinctive species group. All seven species have shells with strongly bicarinate whorls, at least on the first several whorls; have, at the beginning of the first teleoconch whorl, an adapical spiral cord that becomes weak or disappears on subsequent whorls; have a weak angulation or strong spiral cord below the peripheral cord; have the inner lip of the columella weakly or strongly reflected over the umbilicus, or thickened and filling the umbilicus with callus; and have the columella rounding into the outer lip. Other species that may belong to this group include *C. cubanum* Clench & Aguayo, 1940, and the eastern Atlantic *C. grimaldii* Dautzenberg & Fischer, 1896; *C. leptophyma* Dautzenberg, 1927; *C. normani* Dautzenberg, 1927; and *C. caroli* Dautzenberg, 1927.

Calliostoma dnopherum (Watson, 1879),
new combination
(figures 67–69)

Trochus (*Margarita*) *dnopherus* Watson, 1879:711; 1886:90, pl. 5, fig. 3

Figures 53–56. *Calliostoma vinosum* new species. **53, 54.** Holotype, MORG 29 294; height 13.5 mm, width 15.3 mm. **55, 56.** Paratype, MORG 15 043; height 10.2 mm, width 11.9 mm. **Figures 57, 58.** *Calliostoma alternum* new species, holotype, USNM 860257; height 15.6 mm, width 13.9 mm. **Figures 59–62.** *Calliostoma aulicum* new species. **55, 56.** Holotype, USNM 860258; height 15.9 mm, width 16.1 mm. **57, 58.** Paratype from JOHN ELLIOTT PILLSBURY Station P-669, UMML 30.8375; height 10.8 mm, width 11.2 mm. **Figures 63, 64.** *Calliostoma hirtum* new species, holotype, USNM 860260; height 17.9 mm, width 19.8 mm.



Figures 67–69. *Calliostoma dnopherum* (Watson, 1879). Lectotype of *Trochus* (*Margarita*) *dnopherus*, BM(NH) 1887.2.9.333, height 7.2 mm, width 5.5 mm.

Margarites dnopherus: Lange de Morretes, 1949:55
"Margarites" dnopherus: Rios, 1955 19, pl. 5, fig. 72.

Description: See Watson (1879:711; 1886:90).

Lectotype (here selected): BM(NH) 1887.2.9.333, height 7.2 mm, width 8.8 mm.

Type locality: Southeast of Recife, Brazil, CHALLENGER Station 122, 9°05'S, 34°49'W, in 640 m.

Paralectotypes: 4 (broken or fragments), BM(NH) 1887.2.9.334–335; from same lot as holotype.

Other material: 1, Coltro collection; off Ilha de São Sebastião, Estado de São Paulo, Brazil, 600 m; dredge; 1991.

Distribution: This species is now known from off Recife to off São Paulo, Brazil (a range extension of approximately 2000 km), in 600–640 m.

Remarks: The shape and sculpture of the shells of this species are very similar to those of *C. rota*, *C. atlantoides*, and *C. coronatum* (*q. v.*); therefore, the species is here transferred to *Calliostoma sensu lato*. Shells of *C. dnopherum* differ from those of *C. rota* by being somewhat higher and more globose, by having a larger protoconch (825–850 μm *vs.* 400–425 μm), by having a strong spiral cord midway between the shoulder spiral cord and the circumbasal cord, by having a strong spiral cord just beneath the circumbasal cord, and by having an open umbilicus. Differences between *C. dnopherum* and *C. atlantoides* and *C. coronatum* are discussed in the Remarks in the species accounts of the latter two species.

The syntype lot originally contained five specimens, one large, live-collected specimen and four very small shells. The large shell is in excellent condition, although the animal was removed at some point and the operculum glued to cotton in the aperture. Of the four small shells, one has completely disintegrated, and the other three are in various stages of disintegration.

The recently collected specimen (Coltro collection) is very similar to the lectotype but is slightly smaller (7.0 mm height, 8.5 mm width), lacks fine threads between the supraperipheral spiral cords, has one fewer basal

spiral cord, and has the inner lip of the columella rather strongly expanded to almost cover the umbilicus.

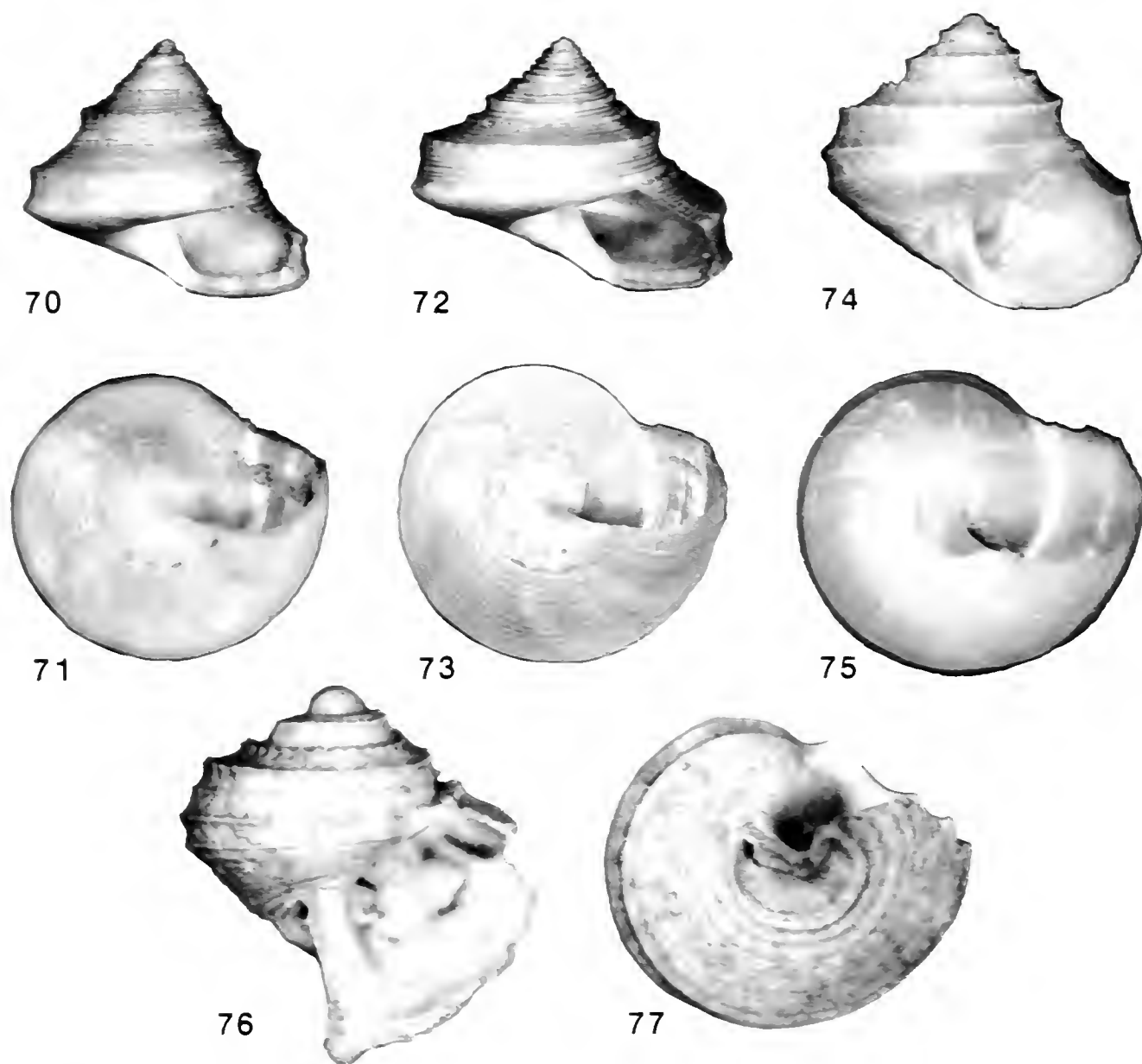
Calliostoma rota new species
 (figures 70–73, 117, 118)

Description: Shell small, attaining height of 8.1 mm, width of 9.9 mm, depressed turbate, nonumbilicate. Protoconch 400–425 μm maximum diameter, 1 whorl. Teleoconch whorls 5.5, rapidly expanding, carinate; first whorl initially with 2 smooth spiral cords; adapical cord strong on first 2 whorls, gradually weakening to fine thread on next 3 whorls, finely undulate to beaded on last 3 whorls; abapical cord strong, smooth to weakly undulate on all whorls, forming carinate whorl shoulder; subsutural cord appearing on first quarter-whorl, becoming strong, finely beaded by third whorl; last whorl with strong, smooth, circumbasal spiral cord forming peripheral carina; interspaces between spiral cords concave with fine, smooth or finely beaded spiral threads (last whorl with 11–12 between subsutural and shoulder cords, 8–14 between shoulder and peripheral cords); axial sculpture absent except fine growth lines. Base almost flat, with 17–21 weak to strong, flat, smooth spiral cords and 0–4 fine threads in interspace between peripheral cord and outermost basal cord; outermost cord sometimes forming very weak subperipheral angulation. Umbilicus filled with callus. Aperture subquadrate; outer lip thin, angulate; inner lip thickened, forming umbilical plug; columella rather short, concave in upper third, straight below. Shell ground color ivory to pinkish tan with green and pink iridescence, with regularly spaced spots of light to dark yellow-brown on subsutural, shoulder, peripheral, and 1–2 inner basal cords, basal cords sometimes lacking spots.

Holotype: MORC 29.295, height 8.1 mm, width 9.3 mm.

Type locality: Off Ilhabela, Ilha de São Sebastião, Estado de São Paulo, Brazil, in 20–30 m.

Paratype: 1, MCZ 258057; off Rio de Janeiro, Estado de Rio de Janeiro, Brazil, from stomach of starfish, in about 46 m; Bernard Tursch collector.



Figures 70–73. *Calliostoma rota* new species. 70, 71. Holotype, MORC 29295, height 8.1 mm, width 9.3 mm. 72, 73. Paratype, MCZ 258057, height 7.6 mm, width 9.9 mm. Figures 74, 75. *Calliostoma atlanticoides* new species, holotype, USNM 860261, height 9.1 mm, width 10.0 mm. Figures 76, 77. *Calliostoma ornatum* new species, holotype, MCZ 274568, height 4.2 mm, width 4.2 mm.

Other material: 1. Coltro collection, from same lot as holotype.

Distribution: This species is known only from off Rio de Janeiro and São Paulo, Brazil, in 20–46 m, the single living specimen was from 46 m.

Remarks: Shells of *Calliostoma rota* are most similar to those of *C. dnopherum* but differ by having more whorls, by having a much smaller protoconch, by lacking a strong spiral cord between the shoulder and circum-

basal cords, by lacking a strong subperipheral spiral angulation, and by having the umbilicus filled with callus. The radula of *C. rota* (formula 12–13.7 1.7 12–13; figures 117, 118) has two principal characters that depart from the typical calliostomatine morphology: 1. the reduced number of elements in the marginal tooth field, and 2. the single, uncusped tooth base representing the outer lateral tooth. The number of pairs of calliostomatine marginal teeth is rarely reported, but in those instances where the number of pairs is known (e.g., Calvo, 1987,

the number is 25 or more except in *Astele* Swainson, 1855, the type species of which has about 20 pairs (Clench & Turner, 1960:76); however, in *C. rota* there are only 12 or 13 pairs. The presence of a single, uncusped outer lateral tooth has not been reported previously in the Calliostominae, although this condition bridges the gap between the majority of species that have all lateral teeth cusped and those in the *C. jujubinum* species group that have the outer two pairs of lateral teeth uncusped. However, although the anterior two-thirds of the radula examined here had the uncusped lateral tooth, a few teeth from the posterior third retained a membranaceous, rudimentary cusp. The holotype and Coltro specimen were dredged from muddy sand bottom.

Calliostoma atlantoides new species
(figures 74, 75, 115, 116)

Description: Shell small, attaining height of 9.1 mm, width of 10.0 mm, turbinate, narrowly umbilicate. Protoconch 1.10 mm maximum diameter, 1 whorl. Teleoconch whorls 3.4, rapidly expanding, carinate; first whorl initially with 2 smooth, spiral cords, adapical cord disappearing by end of first whorl, abapical cord strengthening and forming strong midwhorl carination on subsequent whorls; third spiral cord appearing between adapical cord and suture near beginning of first whorl, strengthening and forming rather strong subsutural angulation; both subsutural and midwhorl angulations set with narrow, rounded, spirally elongate beads; last whorl with strong, smooth spiral cord forming periphery; interspaces between spiral angulations weakly concave, with fine, smooth spiral threads (last whorl with 2 between suture and subsutural angulation, 16 between subsutural and midwhorl angulations, and 12 between midwhorl and peripheral angulations); axial sculpture of low, rounded riblets restricted to first 1.25 whorls. Base divided into narrow, weakly concave peripheral zone and broad, weakly convex central zone by strong spiral cord; peripheral zone with 6 spiral threads, central zone with about 18 weak, smooth spiral cords. Umbilicus funnel-shaped, broad, about 25% maximum shell diameter, wall strongly constricted to narrow pore. Aperture obscurely subquadrate, almost elliptical; outer lip thin, slightly angulate; inner lip thin and expanded above to partially cover umbilicus, becoming narrower and thicker below; columella concave in upper and lower quarters, almost straight in middle half, narrow above but broad and weakly concave at base, with prominent adapical nacreous tongue. Shell ground color silvery white with brilliant pink and green iridescence.

Holotype: USNM 860261, height 9.1 mm, width 10.0 mm.

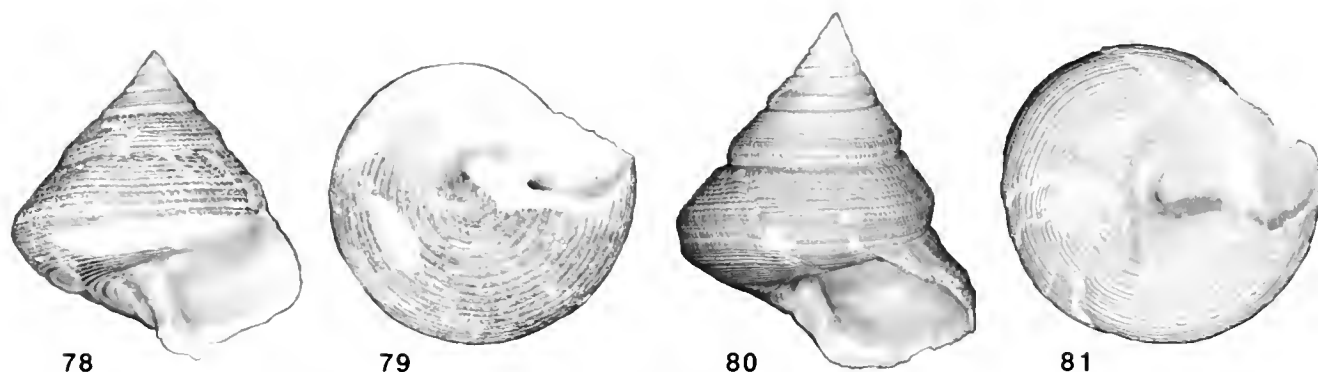
Type locality: West of St. Lucia, Lesser Antilles, JOHN ELLIOTT PILLSBURY Station P-904, 13°45.5'N, 61°05.7'W, in 417–589 m.

Distribution: This species is known only from the type locality.

Remarks: In shell shape and sculpture, *Calliostoma atlantoides* is most similar to *C. coronatum* new species but differs by having a larger protoconch, by having the beads on the subsutural spiral cord weaker and more widely spaced, by having numerous spiral threads in the interspaces, by having a strongly beaded rather than finely undulate shoulder spiral cord, by having weaker and more numerous basal spiral cords, and by having the inner columellar lip expanded to partially cover the umbilicus. The shell of *C. atlantoides* is also very similar to those of *C. rota* and *C. dnopherum*. It differs from that of *C. rota* by being relatively higher and more globose, by having a much larger protoconch, by having a more coarsely beaded subsutural spiral cord, by having a strongly beaded rather than smooth shoulder spiral cord, by having an open umbilicus, and by being silvery white rather than slightly brassy. The shell of *C. atlantoides* differs from those of *C. dnopherum* by being relatively higher; by having a larger protoconch; by having a single, beaded spiral cord rather than two smooth spiral cords below the subsutural cord; by having finer, more numerous spiral threads in the interspaces; by having more numerous basal spiral cords; and by having the inner lip of the columella thinner and more strongly expanded to partially cover the umbilicus. *Calliostoma atlantoides* is similar to *C. atlantis* but has a much smaller, more globose shell; has a much larger protoconch; has the shoulder spiral cord located much higher on the whorl; has a much stronger subperipheral angulation; and has the inner lip of the columella thin and partially covering the umbilicus rather than being thickened and completely filling the umbilicus. The radula of *C. atlantoides* (formula <20.5? 1.5? <20; Figures 115, 116) is very small (length 3.1 mm) and delicate, and there seem to be five, thin-cusped laterals and fewer than 20 pairs of marginal teeth, the innermost of which has a heavily buttressed and rather finely denticulate cusp. The seemingly degenerate radula of *C. atlantoides* is similar to that illustrated for an undescribed species of *Calliostoma* illustrated by Hickman and McLean (1990:fig. 71C).

Calliostoma coronatum new species
(figures 76, 77)

Description: Shell small, attaining height of 4.2 mm, width of more than 4.2 mm, depressed turbinate, umbilicate. Protoconch 850 μ m maximum diameter, 1 whorl. Teleoconch whorls about 2.2, rapidly expanding, carinate; first whorl initially with 3 smooth spiral cords, adapical cord disappearing at whorl 1.3, midwhorl cord strengthening, becoming weakly undulate at whorl 1.3 and forming strong midwhorl angulation, abapical cord remaining weak on all whorls; fourth spiral cord appearing between adapical cord and suture at whorl 0.3, rapidly strengthening, undulate on last half of first whorl, undulations becoming strong, closely set, upturned, triangular beads; last whorl with strong, smooth spiral cord forming periphery; interspaces smooth except for weak spiral cord between midwhorl and peripheral cords; axial



Figures 78, 79. *Calliostoma rugosum* new species, holotype, USNM 860262, height 23.5 mm, width 24.8 mm. **Figures 80, 81.** *Calliostoma torrei* Clench & Aguayo, 1940, holotype, MCZ 135165; height 40.8 mm, width 36.8 mm.

sculpture absent except for low, rather broad, rounded folds on last whorl. Base divided into narrow, smooth, concave peripheral zone and broad, almost flat central zone by strong, smooth spiral cord; central zone with 12 narrow, smooth spiral cords, adaxial 3 somewhat stronger and more widely spaced. Umbilicus rather narrow, less than 20% maximum shell diameter, constricted within to small pore. Aperture probably obscurely subquadrate or ovate, outer lip broken; inner lip thin, narrow, slightly reflected over umbilicus; columella convex, thin.

Holotype: MCZ 27456S, height 4.2 mm, width 4.2+ mm.

Type locality: Off João Pessoa, Brazil, CHAIN Cruise 35, Station 12, 7°09.0'S, 34°25.5'W, in 768–805 m.

Distribution: This species is known only from the type locality.

Remarks: *Calliostoma coronatum* is similar to *C. dno-pherum* but differs by having a relatively smaller, lower-spired shell that has a much weaker spiral cord between the shoulder and peripheral cords, that lacks spiral threads between the primary spiral cords, and that has a proportionately narrower umbilicus.

Calliostoma rugosum new species
(figures 78, 79)

Description: Shell medium-sized to large, attaining estimated height of 25 mm, estimated width of 31 mm, trochoid, nonumbilicate. Protoconch worn, at least 550 μ m maximum diameter, 1 whorl. Teleoconch whorls about 7.5 (last 0.5 whorl broken), flat to weakly concave; first 2 whorls worn and partially decorticated; whorls 3–4 with 5 strong, subequal, beaded spiral cords, adapical cord forming weak subsutural angulation, abapical cord forming upper limit of flat periphery bearing 1 spiral thread; subsutural and upper peripheral cords each splitting into 2 subequal spiral cords on whorls 5–6; spiral cords between subsutural and upper peripheral cords increasing to 7 by end of seventh whorl; peripheral zone with 4 spiral cords by end of seventh whorl, periphery

becoming rounded on last whorl; all cords set with rather strong, rounded, generally spirally elongate beads. Base weakly convex, with 19 strong, smooth, subequal spiral cords. Umbilical area filled with irregularly ridged callus. Aperture subquadrate; outer lip broken; inner lip thickened; columella concave, broken basally.

Holotype: USNM 860262, height 23.5+ mm, width 24.8+ mm.

Type locality: Straits of Florida, JAMES M. GILLIS Cruise 7307, Station 13, depth and exact locality unknown.

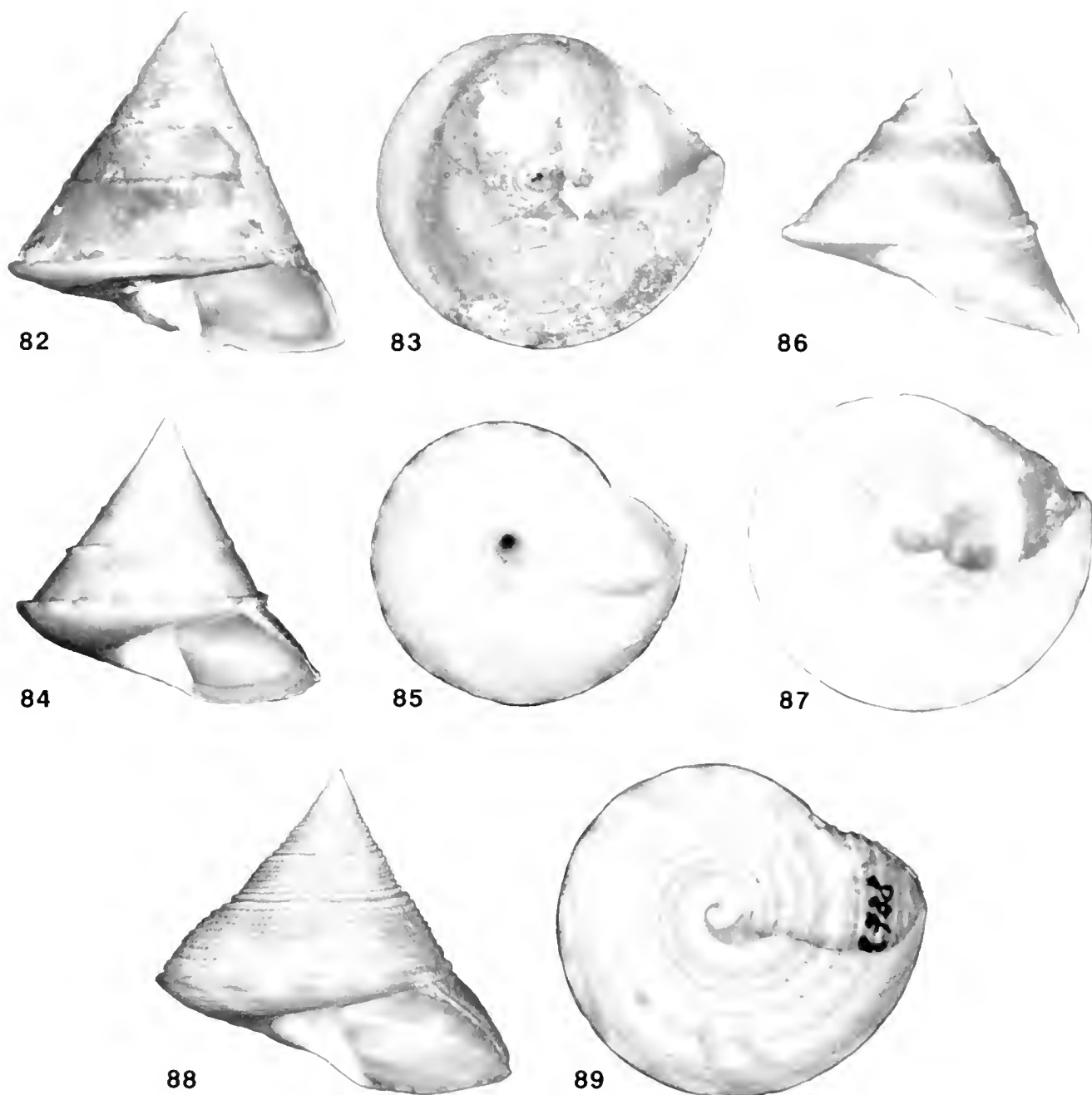
Distribution: This species is known only from the type locality.

Remarks: The holotype of *Calliostoma rugosum* is very similar to that of *C. torrei* Clench and Aguayo, 1940 (figures 80, 81), from off Cárdenas, Cuba, but differs by being relatively much broader; by having a weaker, more abapical upper peripheral cord; by having coarser, more rounded spiral cords; and by having larger, rounded, spirally elongate beads on the cords. The protoconch of *C. rugosum* (estimated to be more than 550 μ m) may be larger than that of *C. torrei* (about 525 μ m), and the subsutural and upper peripheral cords of *C. rugosum* split into two rather coarse cords rather than three fine, sharp cords as in *C. torrei*. Both *C. rugosum* and *C. torrei*, based on similarities of shape and sculpture, seem to be closely related to *C. caribbeanum* Weisbord, 1962, a fossil species from the Pleistocene Mare Formation of Venezuela.

Calliostoma argentum new species
(figures 82–85)

Calliostoma marionae: Sander & Lalli, 1982 table 4 (Non *Calliostoma marionae* Dall, 1906).

Description: Shell medium-sized, attaining height of 25.6 mm, width of 28.2 mm, conical, umbilicate, finely sculptured to almost smooth. Protoconch about 375 μ m maximum diameter, 1 whorl. Teleoconch whorls about 9.5, flat to very weakly convex; first 2 whorls with low, rounded axial riblets and 2–3 finely beaded spiral cords;



Figures 82–85. *Calliostoma argentum* new species. **82, 83.** Holotype, USNM 860263; height and width 18.1 mm. **84, 85.** Specimen from off Barbados, Sunderland collection; height 22.5 mm, width 24.2 mm. **Figures 86, 87.** *Calliostoma jeanneae* Clench & Turner, 1960, holotype, MCZ 228370; height 11.2 mm, width 13.2 mm. **Figures 88, 89.** *Calliostoma axelrothi*, new name, specimen from off Mostardas, Brazil, MORC 18738, height 30.4 mm, width 34.2 mm.

axial sculpture absent on subsequent whorls; spiral cords increasing by intercalation to 9–11, beading disappearing on fourth or fifth whorl but sometimes reappearing on eighth or ninth whorl; periphery sharply carinate, smooth, sometimes reflected adapically. Base flat to weakly convex, with 13–15 weak, broad, smooth spiral cords, adaxial 2–3 cords slightly stronger, weakly beaded; circumumbilical cord strong, coarsely beaded. Umbilicus funnel-

shaped, 14%–17% maximum shell diameter, wall almost vertical, white. Aperture subquadrate, slightly thickened within and with several low, rounded ridges, lips thin; columella rather long, weakly concave, slightly thickened, terminating in small, rounded tubercle. Shell ground color cream to light tan with pale orange-brown patches below suture and spots on periphery; base uniformly cream.

Holotype: USNM 860263, height and width 18.1 mm.

Type locality: Arrowsmith Bank, Quintana Roo, Mexico, JOHN ELLIOTT PILLSBURY Station P-594, 21°00.5'N, 86°23.0'W, in 307–329 m.

Paratypes: 1, UMMIL 30.5583; off Arrowsmith Bank, Mexico, JOHN ELLIOTT PILLSBURY Station P-584, 21°02.0'N, 86°24.0'W, 353–347 m; 23 May 1967; 10-ft otter trawl.—1, ANSP 353529; off Holetown, Barbados; F. Sander, collector.

Other material: 1 fragment, UMMIL 30.8372; off St. Vincent, JOHN ELLIOTT PILLSBURY Station P-877, 13°16.7'N, 61°05.6'W, 348–466 m; 6 July 1969; 5-ft Blake trawl.—3, Sunderland collection; off St. James, Barbados, 175 m; dredge; F. Sander, collector.

Distribution: Shells of *Calliostoma argentum* are known from off the Yucatán Peninsula, Mexico, and St. Vincent and Barbados, Lesser Antilles, in depths of 175–466 m.

Remarks: Shells of *Calliostoma argentum* are most similar to the holotype of *C. jeanneae* (figures 86, 87), from off Havana, Cuba, but differ by being relatively narrower; by having spiral cords that are strongly beaded until the middle of the fourth or fifth whorls rather than becoming smooth near the beginning of the third whorl; by lacking a strong spiral cord just above the periphery on the third through sixth whorls; by having an umbilicus that is open rather than filled with callus; by having a strongly beaded rather than smooth circumumbilical cord; and by having a longer, less thickened and oblique columella. Perhaps of less importance are differences in the color patterns: that of *C. argentum* consists of cream to light tan spiral cords separated by darker-colored striae and pale orange-brown patches below the sutures and somewhat darker spots on the periphery; that of *C. jeanneae* consists of rows of golden-brown spots on the spiral cords above and below the periphery and brighter spots of the same color on the periphery. Both *C. argentum* and *C. jeanneae* are similar to the eastern Pacific *C. platinum*, *C. chilena*, and *C. titanium*, and all five species may be closely related to *C. metalium* Woodring, 1957, from the late Miocene to early Pliocene Chagres Sandstone of Panamá.

Calliostoma axelolssoni new name
(figures 88, 89, 119)

Calliostoma olssoni Bayer, 1971:118, fig. 4 (left).—Kaicher, 1980:card no. 2239. (Non *Calliostoma olssoni* Maury, 1925).

Calliostoma (*Kombologion*) *rosewateri* Rios, 1975:23, pl. 5, fig. 59.—Calvo, 1987:63, 65, fig. 28. (Non *Calliostoma rosewateri* Clench & Turner, 1960).

Calliostoma (*Kombologion*) *bairdi rosewateri* Rios, 1955:22, pl. 9, fig. 85

Description: See Bayer (1971:118) for description of shell. Animal (in alcohol) white; mantle edge smooth; cephalic tentacles moderately long, slender, gradually tapering, right longer than left, ocular peduncles rather

long (about 35% tentacle length), broad, with large, black eye at tips; snout long, broad, slightly expanded at tip, tip fringed with small, short papillae; epipodium with 4 pairs of tentacles decreasing in size posteriorly, neck lobes well-developed, semicircular, smooth.

Holotype: USNM 700002, height 16.8 mm, width 21.0 mm.

Type locality: Southwest of St. Vincent, Lesser Antilles, JOHN ELLIOTT PILLSBURY Station P-876, 13°13.9'N, 61°04.7'W, in 231–238 m.

Other material: 1, UMMIL 30.8373; off Dominica, JOHN ELLIOTT PILLSBURY Station P-931, 15°31.2'N, 61°12.3'W, 174–357 m; 15 July 1969; 5-ft Blake trawl.—1, MORG 18.738; W. Besnard station, off Mostardas, Rio Grande do Sul, Brazil, 230 m; 1972.

Distribution: This species is now known from off Dominica and St. Vincent in the Lesser Antilles, and off southern Brazil, in 174–357 m.

Remarks: *Calliostoma olssoni* Bayer, 1971, is preoccupied by *C. olssoni* Maury, 1925, a species (probably assignable to *Calliomphalus* Cossmann, 1888) from the Mio-Pliocene formations of Trinidad (Maury, 1925; Jung, 1969). With F. M. Bayer's permission, I offer a replacement name that preserves his original intent to honor the late Dr. Axel A. Olsson.

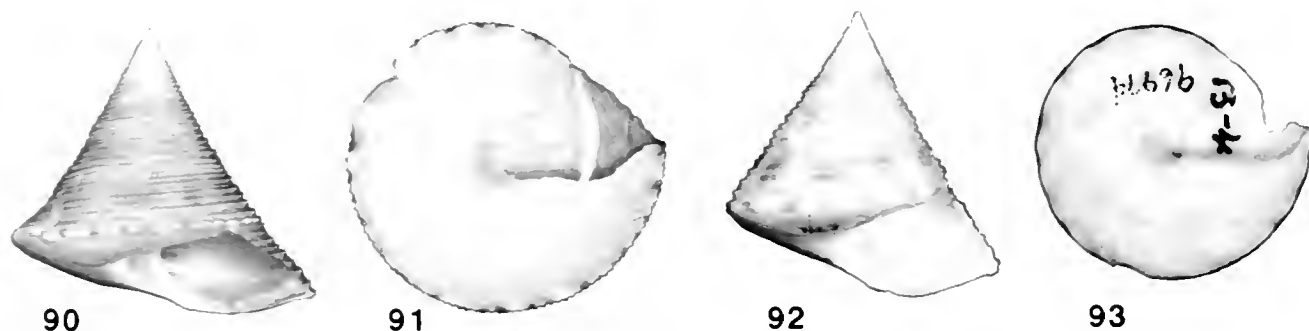
The Brazilian specimen (misidentified as *C. rosewateri* by Rios, 1975, 1985) (figures 88, 89) is much larger (height 30.4 mm, width 34.2 mm) than the holotype, has a narrower umbilicus that has been partially filled with callus, has three weak circumumbilical and six weak subperipheral spiral cords, and has a more diffuse and subdued color pattern except for the pink spots on the periphery. The Dominican specimen is very similar to the holotype but is slightly larger (height 19.9 mm, width 24.1 mm), has a slightly narrower umbilicus, and has a much less vivid color pattern. The radula from this specimen (figure 119) conforms well with Calvo's illustration (1987:fig. 28) but the lateral tooth cusps are longer than he depicted.

Based on shell characters, *C. axelolssoni* seems to be closely related to *C. bigelowi*, *C. brunneum*, and *C. hendersoni*—the four species forming a rather distinct subgroup of *Calliostoma*. This subgroup may be most closely related to the *C. bairdii* species group.

Calliostoma aurora Dall, 1888
(figures 90, 91, 120)

Calliostoma aurora Dall, 1888:68, fig. 285; 1889a:366, pl. 37, fig. 2.—Clench & Turner, 1960:64, pl. 45, figs. 1, 2.

Description: Shell: see Dall (1889a:366) and Clench and Turner (1960:64). Animal (reconstituted in trisodium phosphate): foot mottled with red-brown, mantle edge with light, transverse band and long, median longitudinal streak of red-brown; cephalic tentacles very long, slender; eyestalks very short (less than 10% tentacle length)



Figures 90, 91. *Calliostoma aurora* Dall, 1855, specimen from off Guadeloupe, USNM 860504, height 25.4 mm, width 27.8 mm. Figures 92, 93. *Calliostoma guesti* new species, holotype, DMNH 96994, height and width 27.5 mm.

with large, black eye at tips; snout slightly longer than broad, tip fringed by rather long, stout papillae; epipodium with 3 or 4 pairs of very long, slender tentacles; neck lobes very well-developed, seemingly smooth-edged.

Holotype: MCZ 73505, height 21.0 mm, width 26.5 mm.

Type locality: Off Grenada, Lesser Antilles, BLAKE Station 265, 12°03'55"N, 61°49'40"W, in 1054 m.

Other material: 1. USNM 860504, off Great Inagua Island, Bahama Islands, JOHNSON-SEA-LINK I Station JSL-1-2323, 21°01'45"N, 74°43'48"W, 625 m; 15 October 1955.—1, Dan collection; off Barbados, Lesser Antilles, 153 m.

Distribution: *Calliostoma aurora* is now known from the southeastern Bahama Islands and from off Barbados, in depths of 153–1054 m.

Remarks: The present specimens agree well with the holotype in most shell characters, but are larger (Great Inagua: height 25.4 mm, width 27.5 mm; Barbados: height 23.5 mm, width 27.2 mm); have whorls with flatter profiles; and have numerous very fine spiral striae on the outer two-thirds of the base, the striae becoming deeper on the adaxial third and forming several indistinct and three distinct spiral cords near the center. The ground color of the new shells is a dark golden brown with alternating spots of white and brown on the periphery; the base of the Barbados specimen has faint, crescent-shaped streaks of pale brown; and the umbilical callus of both specimens is white.

Although Clench and Turner (1960) compared the shell morphology of *C. aurora* to that of *C. bairdii* and *C. psyche*, the relationship of this species to other *Calliostoma* species is unclear. The radula of *C. aurora* (formula $\propto 10 \ 1 \ 10 \propto$, figure 120) indicates that the species is not very closely related to the *C. bairdii* species group or to any other western Atlantic species group. The most notable difference is that *C. aurora* has ten pairs of lateral teeth, whereas most other species have only four to seven pairs; only *Calliostoma militare* (22 pairs; Castellanos & Fernandez, 1976; Calvo, 1987) and *Venustatrochus georgianus* (16 pairs; Powell, 1951) have more lateral tooth pairs. The inner marginal teeth of *C. aurora* are also rather unusual: the innermost marginal

is rather slender with a sharply curved cusp and ten denticles, of which the terminal one is unusually long, and the next several teeth have a very long terminal denticle with four to six secondary denticles about a third of the way down the shaft.

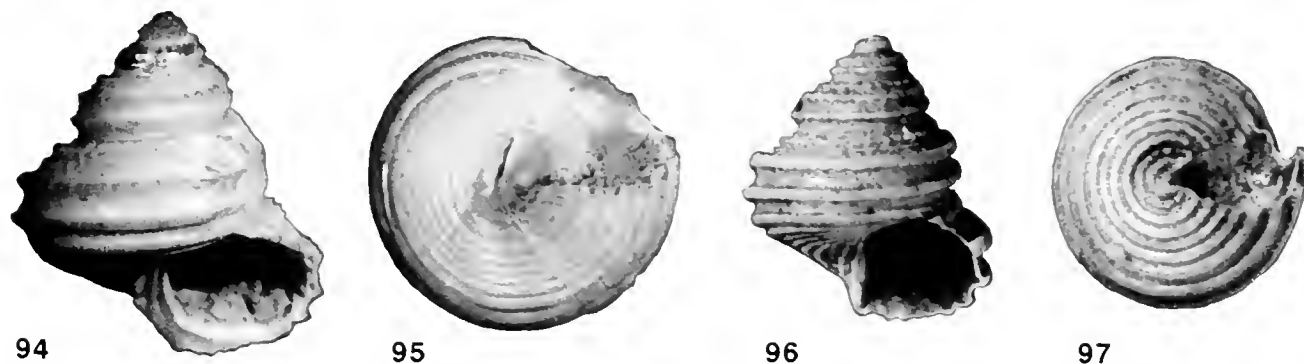
The Barbados specimen was collected alive from a depth of 153 m, which is shallower than, but comparable to, the provenance of the paratype lot (from Barbados in 256 m), suggesting that the occurrence of the holotype in 1054 m was adventitious. The specimen from Great Inagua was collected from atop a small, blue sponge (M. G. Harasewych, personal communication), and its intestine was packed with a dark brown, rather solid mass of organic material in which were embedded numerous sponge spicules and polychaete setae, suggesting that this species feeds on sponges.

Calliostoma guesti new species
(figures 92, 93)

Description: Shell medium-sized, attaining height and width of 27.5 mm, conical, nonumbilicate, finely sculptured. Protoconch about 425 μ m maximum diameter, 1 whorl. Teleoconch whorls more than 9.1, flat to weakly convex; first 2 whorls with low, rounded axial riblets and 2–3 beaded spiral cords; axial sculpture absent on subsequent whorls; spiral cords increasing by intercalation to 12, finely beaded throughout; periphery sharp, narrowly bicarinate, peripheral cords adpressed, adapical peripheral cord distinctly stronger than abapical peripheral cord. Base weakly convex, with numerous fine striae on outer three-fourths and 3–4 weak, weakly beaded spiral cords near center. Umbilicus filled with white callosus. Aperture subquadrate, lips thin, weakly crenulate; columella rather short, weakly concave, thickened. Shell ground color ivory with irregular, diffuse patches of golden brown above periphery, somewhat more discrete spots of same color on periphery; base with very faint, crescent-shaped, radial streaks of light brown and sometimes a few spots on 1–2 spiral cords.

Holotype: DMNH 96994, height and width 27.5 mm.

Type locality: 2.5 mi off south shore of Bermuda, in 183–219 m.



Figures 94–97. *Calliostoma stirophorum* (Watson, 1879) **94, 95.** Holotype of *Trochus (Zizyphinus) stirophorus* Watson, 1879, BM(NH) 1887.2.9.210, height 7.5 mm, width 6.6 mm **96, 97.** Holotype of *Calliostoma arestum* Dall, 1927, USNM 108412, height 5.4 mm, width 5.0 mm

Paratypes: 3, DMNH 187588; 1, USNM 860270; from same lot as holotype.

Distribution: This species is known only from the type locality.

Remarks: Shells of *Calliostoma guesti* are most similar to those of *C. psyche* but differ by being relatively narrower; by having more finely beaded spiral cords; by having the suprapерipheral spiral cord on all whorls sharply beaded and stronger than the subsutural cord rather than being smooth on the first two to three whorls and weaker than the subsutural cord; by having the periphery composed of two adpressed spiral cords, of which the adapical cord is distinctly stronger, rather than having the cords subequal and separated by a concave interspace that is as wide or wider than the cords; by having much weaker spiral and radial sculpture on the base; and by having a color pattern of light brown rather than rose, particularly on the periphery.

Calliostoma guesti is named in honor of Mr. Arthur Guest for his contributions to the knowledge of the molluscan fauna of Bermuda.

Calliostoma stirophorum (Watson, 1879)
new combination
(figures 94–97)

Trochus (Zizyphinus) stirophorus Watson, 1879:695, 1886:59, pl. 6, fig. 2.

Calliostoma arestum Dall, 1927b:127.—Johnson, 1934:70.—Clench & Turner, 1960:79.—Abbott, 1974:46.

Description: See Watson (1879:695; 1886:59).

Holotypes: BM(NH) 1887.2.9.210, height 7.5 mm, width 6.6 mm (*Trochus (Zizyphinus) stirophorus*); USNM 108412, height 5.4 mm, width 5.0 mm (*Calliostoma arestum*).

Type localities: Off Culebra Island, Virgin Islands, CHALLENGER Station 24, 18°38'30"N, 64°05'30"W, in 713 m (*Trochus (Zizyphinus) stirophorus*); off southern Georgia, ALBATROSS Station 2415, 30°44'00"N, 79°26'00"W, in 805 m (*Calliostoma arestum*).

Distribution: This species is known only from the two type specimens, one from off Fernandina, Florida, in 805 m, and off Culebra Island, Virgin Islands, in 713 m.

Remarks: Both Watson (1879, 1886) and Dall (1927b) based their respective species descriptions on unique specimens that were empty and somewhat damaged when collected. The specimen of *Calliostoma arestum* (figures 96, 97) is slightly smaller, has fewer whorls, and is more weathered than that of *Trochus (Zizyphinus) stirophorus* (figures 94, 95), but both shells seem to represent the same species. These two shells are most similar to those of *C. circumcinctum* but differ principally by having three strong, rounded, beaded spiral carinae above the suture rather than the two very strong, blade-like carinae of *C. circumcinctum*; the shells of *C. stirophorum* are also proportionately broader than those of *C. circumcinctum*. The shells of both *C. stirophorum* and *C. circumcinctum* are very similar to those of *Otukaia blacki* (Dell, 1956) from New Zealand; *Calliostoma (Otukaia) delli* McLean and Andrade, 1982; from off Chile, and *Otukaia eltanini* Dell, 1990, from Antarctica, and could be included in the genus or subgenus *Otukaia* Icke, 1942, if that taxon gains general acceptance. Some recent authors (Powell, 1979; McLean & Andrade, 1982; Dell, 1990) are now using *Otukaia* at either the genus or subgenus level.

Calliostoma adpersum (Philippi, 1851)
(figures 98–100, 121)

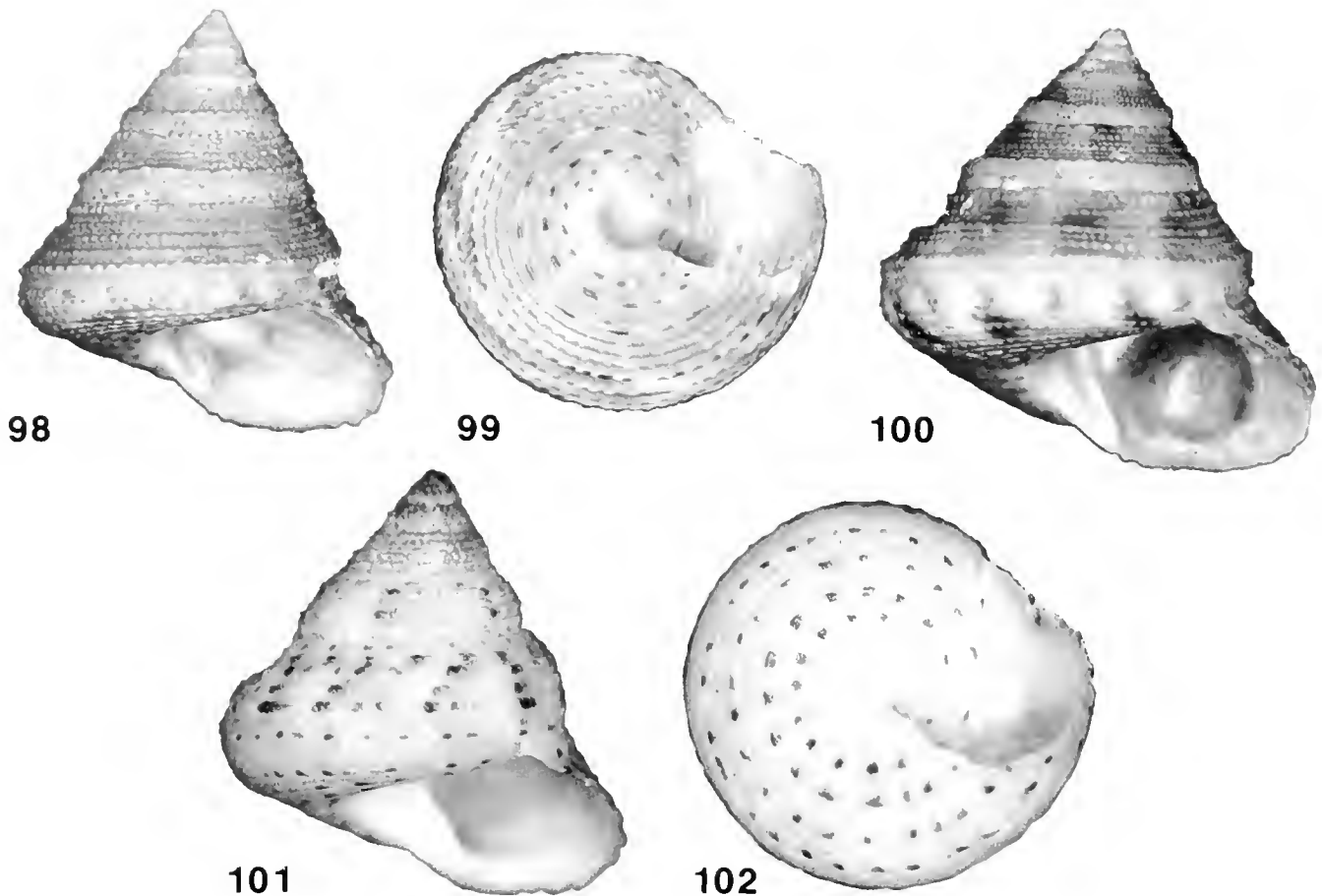
Trochus eximius Philippi, 1844 (in 1842–1851), vol. 1, pt. 6, 17, pl. 4, fig. 7 (Non *Trochus eximius* Reeve, 1843).

Trochus adpersus Philippi, 1851 (in 1846–1855):217, pl. 32, fig. 5.

Calliostoma aspersum: Lange de Morretes, 1949:58.—Calvo, 1987:63, fig. 27. (Unjustified emendation).

Calliostoma adpersum: Calvo, 1987:63, fig. 27.

Calliostoma (Kombologion) adpersum. Clench & Turner, 1960:46, pl. 30, figs. 1, 2 (partim).—Rios, 1970:25, pl. 4 (lower right) (partim); 1975:23, pl. 5, fig. 58, 1985:21, pl. 9, fig. 84, 1990:9, 10 (photographs).



Figures 98–100. *Calliostoma adpersum* (Philippi, 1851), specimens from off Cabo de la Vela, Colombia. **98, 99.** FSBC I 34044; height 17.9 mm, width 18.2 mm. **100.** Deynzer collection; height 16.3 mm, width 15.6 mm. **Figures 101, 102.** *Calliostoma depictum* Dall, 1927, specimen from off Salvador, Brazil, FSBC I 44110, height 10.3 mm, width 9.9 mm.

Description: See Clench and Turner (1960:46) and Rios (1990:9) for descriptions of shells. Animal (in alcohol): foot red-brown; mantle with narrow band of white at edge, behind which is broad, irregularly edged band of brown; cephalic tentacles long, slender, evenly tapered, ocular peduncles stout, about 25% tentacle length, with large, black eye at tips; snout long, broad, expanded at tip, red-brown, with anterior fringe of long papillae; epipodium with 3 pairs of red-brown tentacles, those on left larger, neck lobes well-developed, semicircular, left lobe finely fringed, right lobe smooth.

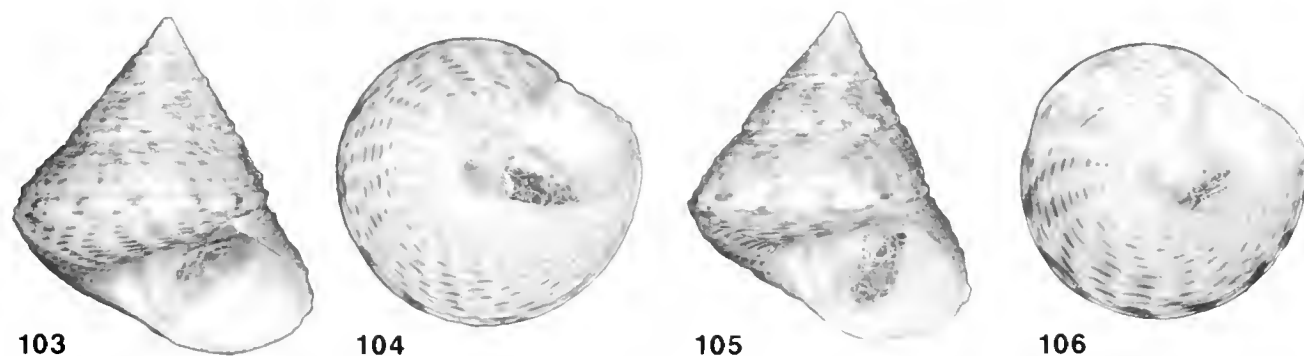
Holotype: Philippi's type material could not be located in the Museum für Naturkunde der Humboldt-Universität zu Berlin (R. Kilias, *in litt.*), and although it may be present in Chile, I consider it to be lost.

Type locality: Restricted by Clench and Turner (1960:47) to Praia do Leste, Ilha Guaíba, Estado de Rio de Janeiro, Brazil

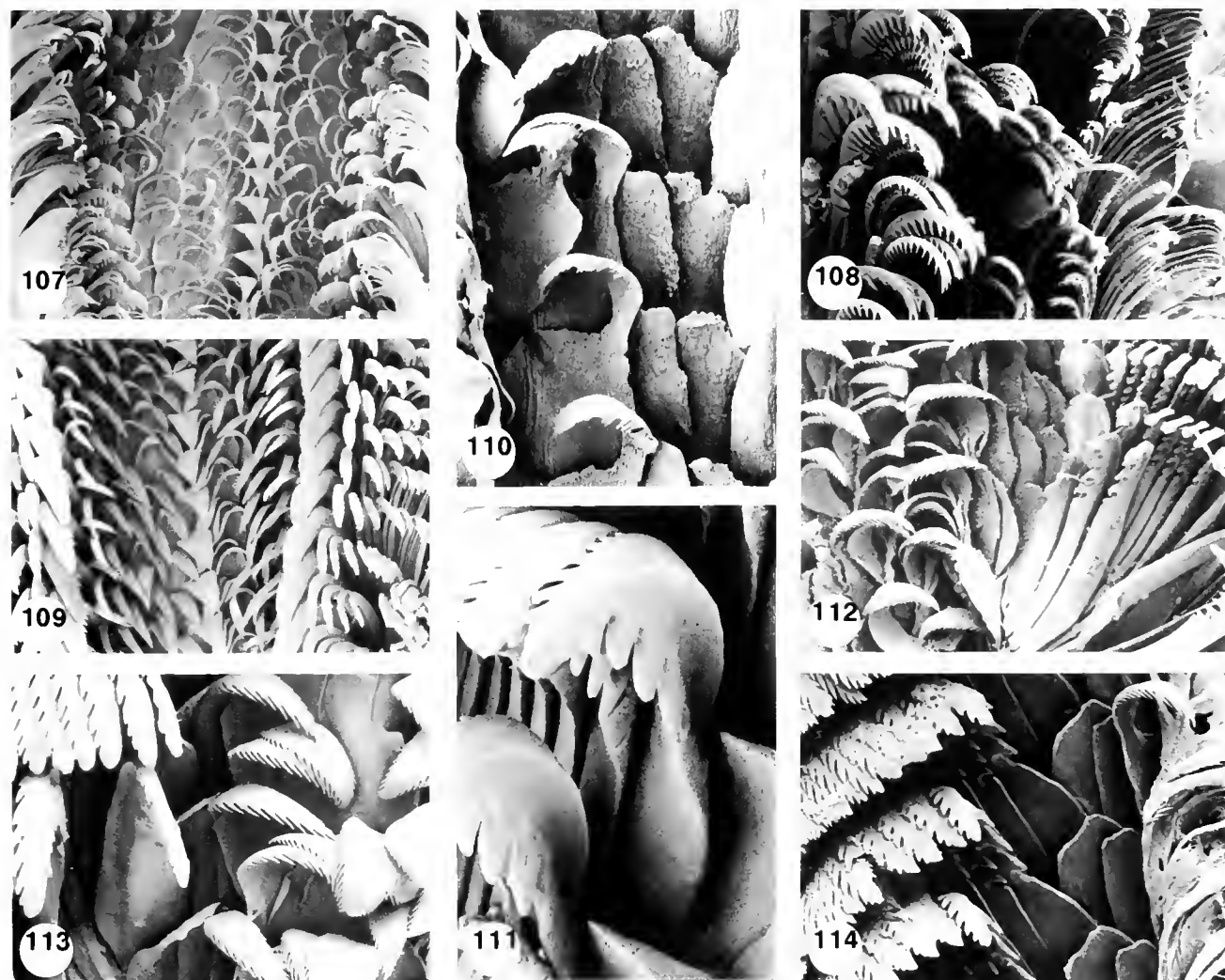
Other material: 1, UMML 30.8365; off Cabo de la Vela, Colombia, JOHN ELLIOTT PILLSBURY Station P-780, 11°39.0'N, 73°08.5'W, 18–27 m; 30 July 1968; 10-ft otter trawl.—1, FSBC I 34044; 21, Deynzer collection; off

Cabo de la Vela, Colombia; 1990; shrimp trawlers.—1, UMML 30.7156; off Cabo de la Vela, Colombia, JOHN ELLIOTT PILLSBURY Station P-767, 12°16.1'N, 71°03.3'W, 24–26 m; 28 July 1968; 10-ft otter trawl.—1, UMML 30.7040; off Península de Paraguaná, Venezuela, JOHN ELLIOTT PILLSBURY Station P-758, 11°42.2'N, 69°40.0'W, 15–18 m; 27 July 1968; 10-ft otter trawl.—1, UMML 30.6888; off Tucacas, Venezuela, JOHN ELLIOTT PILLSBURY Station P-750, 10°36.1'N, 68°12.2'W, 22–26 m; 25 July 1968; 10-ft otter trawl.—2, UMML 30.6617; off Isla de Margarita, Venezuela, JOHN ELLIOTT PILLSBURY Station P-721, 11°06.5'N, 64°22.5'W, 26–27 m; 21 July 1968; 10-ft otter trawl.—1, UMML 30.6183; off Georgetown, Guyana, JOHN ELLIOTT PILLSBURY Station P-686, 7°00.0'N, 57°08.0'W, 27–26 m; 15 July 1968; 10-ft otter trawl.—2, UMML 30.5931; off Cayenne, French Guiana, JOHN ELLIOTT PILLSBURY Station P-655, 6°07.0'N, 53°39.0'W, 26 m; 9 July 1968; 10-ft otter trawl.—4, FSBC I 44109; off Guarapari, Estado de Espírito Santo, Brazil, 18–20 m; March 1991; ex J. & M. Coltro.

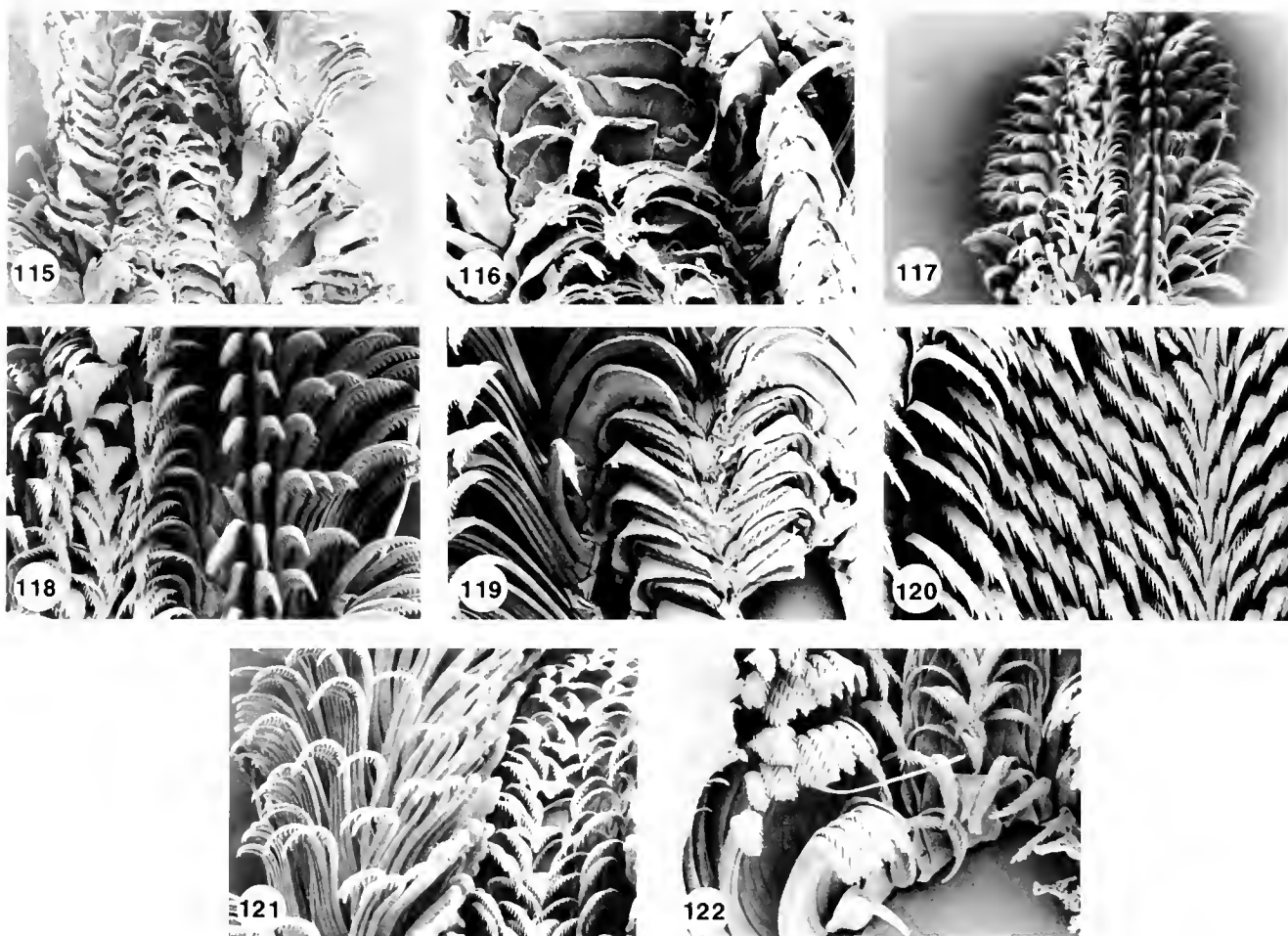
Distribution: *Calliostoma adpersum* was thought to be endemic to Brazil (Clench & Turner, 1960; Rios, 1970, 1975) until Rios (1985) reported its occurrence in Suri-



Figures 103–106. *Calliostoma scurra* new species. **103, 104.** Holotype, USNM 860264, height 14.1 mm, width 13.3 mm. **105, 106.** Paratype from JOHN ELLIOTT PILLSBURY Station P-834, FSBC I 44073; height 13.9 mm, width 12.7 mm.



Figures 107–114. Radulae of *Calliostoma* species. **107.** *Calliostoma cnidophilum* new species, ex paratype, FSBC I 44070; 95 \times . **108.** *Calliostoma viscardii* new species, ex holotype, MORG 29.292, 310 \times . **109.** *Calliostoma moscatellii* new species, ex specimen from off Rio de Janeiro, Brazil, 65 \times . **110, 111.** *Calliostoma scalenum* new species, ex specimen from Campeche Bank, Yucatán, FSBC I 32311; 235 \times and 435 \times , respectively. **112.** *Calliostoma jujubinum* (Gmelin, 1791), ex specimen from Cat Island, Bahama Islands, FSBC I 15698; 125 \times . **113.** *Calliostoma cubense* new species, ex paratype from off Península de Hicacos, Cuba, FSBC I 32405, 245 \times . **114.** *Calliostoma vinosum* new species, ex holotype, MORG 29.294; 280 \times .



Figures 115–122. Radulae of *Calliostoma* species. **115, 116.** *Calliostoma atlantoides* new species, ex holotype, USNM 860261; 75 \times and 160 \times , respectively. **117, 118.** *Calliostoma rota* new species, ex paratype, MCZ 258057; 50 \times and 115 \times , respectively. **119.** *Calliostoma axelolssoni* new name, ex specimen from off Dominica, UMML 30.8373; 65 \times . **120.** *Calliostoma aurora* Dall, 1888, ex specimen from Guadeloupe, USNM 860504; 70 \times . **121.** *Calliostoma adpersum* (Philippi, 1851), ex specimen from off Guarapari, Brazil, FSBC 1 44108; 95 \times . **122.** *Calliostoma depictum* Dall, 1927, ex specimen from off Ilhabela, São Paulo, Brazil, FSBC 1 44109; 190 \times .

name. The present material establishes the presence of the species along the entire northern coast of South America, principally in depths of about 15–30 m.

Remarks: As noted by Rios (1975, 1985, 1990), the names *Calliostoma adpersum* and *C. depictum* (figures 101, 102) do not represent the same species, as was contended by Clench and Turner (1960). Shells of *C. adpersum* attain a larger size; have all whorls with a distinct shoulder angulation and flat-sided periphery; have more numerous, more unequally sized spiral cords; and have more diffuse color patterns than those of *C. depictum*. One juvenile specimen (UMML 30.7156; height 6.5 mm, width 7.3 mm) differs from larger shells by having an open umbilicus whose wall narrows rapidly from 1.6 mm to a pore-like opening only 0.3 mm wide; larger specimens have the umbilicus filled with callus. The radula of *C. adpersum* (figure 121) differs from that of *C. depictum* (figure 122) by having a more broadly cusped rachidian, by having fewer pairs of lateral teeth (4 *vs.*

5, respectively), and by having more numerous (about 40 *vs.* about 25) marginal tooth pairs whose cusps are narrower and have more slender denticles.

This species seems to occur most frequently in areas of “hard bottom” in the western part of its range (JOHN ELLIOTT PILLSBURY field data log) and on sandy mud bottom in the eastern and southern part (Rios, 1985; J. & M. Coltro, personal communication). *Calliostoma depictum* lives in depths of 1–7 m in sandy areas around rocks and corals (Rios, 1990), where it is often found living under an unidentified sea urchin (J. & M. Coltro, personal communication); the species is also found on *Sargassum* (Rios, 1985, 1990).

Calliostoma seurra new species
(figures 103–106)

Description: Shell medium-sized, attaining height of 14.1 mm, width of 13.3 mm, conical, nonumbilicate,

rather coarsely sculptured. Protoconch 400–425 μm maximum diameter, 1 whorl. Teleoconch whorls about 7, weakly convex; first 4 whorls with numerous low, rounded axial riblets and 2–5 finely beaded spiral cords; axial sculpture absent on subsequent whorls; spiral cords increasing by intercalation to 10–15, usually alternating in size, set with crowded, rounded beads; periphery weakly angulate, composed of pair of adpressed spiral cords, adapical cord stronger, beaded, abapical cord smooth. Base convex, with 12–19 strong, narrow, smooth spiral cords, interspace between abaxial 2 cords usually with 1–5 fine spiral threads and next adaxial interspace usually with 1 thread. Umbilicus filled with callus, shallow depression sometimes present. Aperture subquadrate, thickened within, often with channel corresponding to periphery, lips thin, weakly crenulate; columella very weakly concave, greatly thickened, with tongue of nacre extending outward to umbilical callus. Shell ground color cream with spots and irregular patches of reddish brown above periphery and irregularly crescentic streaks of same color on base.

Holotype: USNM 860264, height 14.1 mm, width 13.3 mm.

Type locality: Off mouth of Orinoco River, Venezuela, JOHN ELLIOTT PILLSBURY Station P-834, 9°04.1'N, 60°10.7'W, in 33–35 m.

Paratypes: 1, USNM 860265; 1, FSBC I 44073; 1, UF 189457; 1, MCZ 302590; 1, ANSP 389338; 1, LACM 2253; 4, UMML 30.7225; all from same lot as holotype.

Other material: 1, UMML 30.6529; off Isla de Margarita, Venezuela, JOHN ELLIOTT PILLSBURY Station P-718, 11°22.5'N, 64°08.6'W, 60 m; 20 July 1968; 10-ft otter trawl.—1, UMML 30.6374; off Península de Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-705, 10°45.0'N, 62°00.0'W, 77–86 m; 18 July 1968; 10-ft otter trawl.—6, UMML 30.6359; Gulf of Paria, Venezuela, JOHN ELLIOTT PILLSBURY Station P-704, 10°34.3'N, 61°57.0'W, 18 m; 18 July 1968; 10-ft otter trawl.—1, UMML 30.6339; off Orinoco River, Venezuela, JOHN ELLIOTT PILLSBURY Station P-696, 8°38.0'N, 58°56.0'W, 55–59 m; 16 July 1968; 10-ft otter trawl.—1 + 1 fragment, UMML 30.5979; off Parimaribo, Suriname, JOHN ELLIOTT PILLSBURY Station P-663, 6°29.0'N, 54°41.0'W, 24 m; 10 July 1968; 10-ft otter trawl.

Distribution: *Calliostoma scurra* has been collected from off Suriname northwestward to off Isla de Margarita, Venezuela, in depths of 18–86 m; live-collected specimens are known from depths of 18–35 m.

Remarks: *Calliostoma scurra* does not seem to be closely related to any other western Atlantic species except, perhaps, *C. adpersum*. Shells of the latter species differ from those of the former by having a broad, flat periphery; by having distinct axial rugae in the interspaces between the primary spiral cords; by having finer, more numerous, more distinctly beaded suprapерipheral spiral

cords; by having a more oblique columella; and by having a different color pattern.

The field data indicate that this species lives on bottoms composed of mud, shell hash, and coral rubble.

ACKNOWLEDGMENTS

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A New Species of *Pseudorimula* (Fissurellacea: Clypeosectidae) from Hydrothermal Vents of the Mid-Atlantic Ridge

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ABSTRACT

Pseudorimula midatlantica new species is described from the Snake Pit hydrothermal field on the Mid-Atlantic Ridge. It is the second member of its genus, the type species being known from the Mariana Trough hydrothermal vents in the mid-Pacific. It differs from the type species in its hypertrophied development of the gonad, which displaces part of the space normally occupied by the foot on the left side; correspondingly, the posterior shell muscle of the type species is merged with the right shell muscle in *P. midatlantica*. Other differences are that it has three rather than six pairs of epipodial tentacles. The new species also provides evidence of faunal interchange between widely separated ridge systems.

Key words: Archaeogastropoda, Fissurellacea, Clypeosectidae; hydrothermal-vent limpets; Mid-Atlantic Ridge.

INTRODUCTION

The slit limpet genus *Pseudorimula* McLean, 1989, was based on a single species from hydrothermal vents at the Marina Trough in the mid-Pacific. Here I add to the genus a second species from the Mid-Atlantic Ridge, a ridge system for which other components of the fauna are largely undescribed. First indications of biota on the Mid-Atlantic Ridge came from camera tows and dredgings by the NOAA vessel *Researcher* at a hydrothermal field at 26°N (Rona *et al.*, 1986); mollusks were not reported. Mollusks from the Mid-Atlantic Ridge were first collected in 1988 by observers on the deep-submersible *Nautila* at the Snake Pit hydrothermal field at 23°N. Spreading centers at these two sites on the Mid-Atlantic Ridge are diverging at a slower rate than those of the East Pacific (Rona *et al.*, 1986; Tunnichliffe, 1991).

Unusual features of the biota of the Snake Pit vents were noted by Mevel *et al.* (1989): "The characteristic feature of these hydrothermal sites is the amazing density of shrimps agglutinated on the chimneys; around the vents, the fauna consists of sea anemones, polychaetes,

gastropods, galatheids, mussels and zoarcid fish. The Snake Pit differs from the Pacific sites mostly by the absence of vestimentiferan worms, alvinellid and serpulid polychaetes and cephalopods."

This new species of *Pseudorimula* came to my attention after the original paper (McLean, 1989) was in press. It adds new limits to the morphology known in the family and provides an example of interchange between widely separated ridge systems. It is also the first mollusk to be documented from the Mid-Atlantic Ridge.

MATERIALS AND METHODS

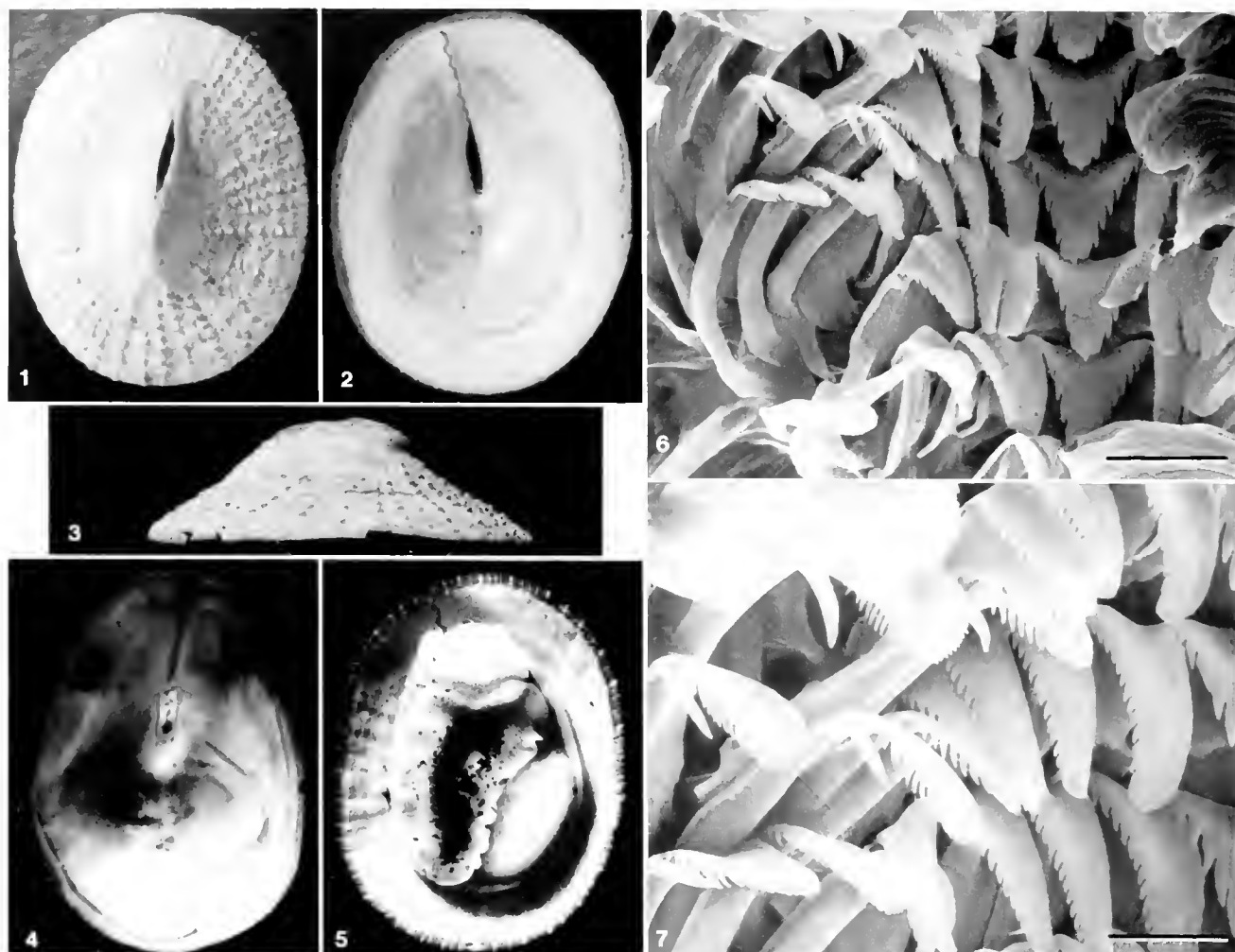
Specimens were collected by the French expedition HYDROSLAKE to the Mid-Atlantic Ridge, June–July 1988, and forwarded to me by Michel Segonzac of the Centre National de Tri d'Océanographie Biologique (CENTOB, IFREMER, Brest).

The illustrated radula was extracted from a preserved specimen after dissolution of tissues with room temperature 10% NaOH for 48 hours, washed in distilled water, air dried and coated with gold palladium for SEM examination.

Abbreviations for museums mentioned in the text are: MNHN, Muséum National d'Histoire Naturelle, Paris; LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, Washington.

Suborder VETIGASTROPODA Salvini-Plawen, 1980
Superfamily FISSURELLACEA Fleming, 1922
Family CLYPEOSECTIDAE McLean, 1989

Clypeosectids differ from fissurellids in having a distinct radular plan, a reduced epipodium, a different pattern of shell musculature, and differences in the internal anatomy, as discussed in more detail by McLean (1989) and Haszprunar (1989). Haszprunar (1989) provided the an-



Figures 1–7. *Pseudorimula midatlantica* McLean, sp. nov. Nautilé dive HS10. Snake Pit hydrothermal field, Mid-Atlantic Ridge, 3,478 m. Holotype, MN11N. Anterior at top in vertical views. 1–3. External, internal, and left lateral views of shell. Length 8.1 mm. 4. Dorsal view of detached body showing left and right shell muscles. 5. Ventral view of body attached to shell, showing protruding gonad on left side of foot. Epipodial tentacles are concealed by the foot in this view. 6, 7. SEM views of radula of paratype. Scale bar for 6 = 20 μ m; scale bar for 7 = 10 μ m.

atomical evidence to justify the erection of a second family in the superfamily Fissurellacea.

On radular characters, the Fissurellidae differ from the Clypeosectidae in having a massive pluricuspid tooth that separates the lateral field of teeth from the marginal teeth. The pluricuspid tooth is lacking in the Clypeosectidae, in which the lateral and marginal teeth are strikingly similar in morphology. *Clypeosectus* McLean, 1989, was established for two species from eastern Pacific vents that have shells with an open slit deflected to the right. *Pseudorimula*, which is convergent in shell morphology with the fissurellid genus *Rimula* de France, 1827, has the slit closed at the margin.

Genus *Pseudorimula* McLean, 1989

Pseudorimula McLean, 1989:22. Type species: *Pseudorimula marianae* McLean, 1989.

Pseudorimula midatlantica McLean, spec. nov.
(figures 1–7)

Pseudorimula sp. McLean; Martin & Hessler, 1990:10; Tunnicliffe, 1991:349.

Description: Shell (figures 1–3) relatively large for family, maximum length 8.1 mm. Surface coated with rusty mineral deposits, under which periostracum yellowish brown, tightly adhering, projecting slightly past shell margin. Outline of aperture oval, margin of aperture nearly in same plane; highest elevation of shell at about one-half its length. Profile moderately high, height of holotype 0.34 times length. Apical whorl at two-thirds shell length from anterior end, slightly deflected to right; protoconch diameter 150 μ m. First teleoconch whorl smooth, rounded; slit arising two protoconch diameters away. Juvenile shells with open slit; in mature shells slit open about one-third length of anterior slope, strongly

deflected to right. Borders of foramen raised, except anteriorly, where slit is sealed in mature shells and its trace slightly depressed. Selenizone weakly depressed below slit border, additions to selenizone extending straight across. Sculpture of about 30 well-defined primary ribs with one to three secondary ribs of lesser prominence arising in interspaces. Concentric sculpture of fine growth lines, raised into sharp lamellar scales on crossing primary ribs. Shell interior opaque. Muscle scar well marked on shell interior; left and right arms swollen at anterior tips, but of uneven thickness posteriorly; right arm longer and retaining its thickness to its termination near midpoint; left arm shorter anteriorly and posteriorly, connecting to right arm through narrow band. Anterior pallial attachment scars well marked, extending close to suture bringing two anterior portions into contact anterior to foramen. Suture with zig-zag outline. Shell strengthened by thickened callus adjacent to suture and surrounding foramen.

Dimensions of holotype: Length 8.1, width 6.4, height 2.5 mm.

External anatomy (figures 4, 5): Anterior end of foot with double anterior edge marking opening of anterior pedal gland; foot posterior rounded; left side of foot displaced postero-laterally by projecting gonad. Cephalic tentacles contracted from preservation. Two posterior pairs of epipodial tentacles, on body wall midway between foot edge and thick border of mantle margin (posterior tentacles of right side in cavity abutting projecting gonad); single anterior pair, all with thick, joined bases, each with narrow projecting tips. Mantle skirt deeply emarginate, corresponding to foramen and seam in shell, edge of emargination with projecting papillae. Mantle skirt above head thin, nearly transparent. Shell muscles without inturned hooks; left muscle short in relation to right and truncate, right muscle extending more anteriorly than left, having thick posterior arm extending not quite to midpoint; left and right muscles joined by thin connective muscle near margin. Right ctenidium smaller than left; both ctenidia reduced, having filaments only on inner sides of axes.

Radula (figures 6, 7): Radular ribbon nearly symmetrical. Rachidian tooth with long overhanging tip, edges deeply serrate; shaft of rachidian short but broad at base. Four pairs of lateral teeth, similar in morphology to rachidian except much narrower; outer edges with fine serration, inner edges smooth; size of overhanging tips decreasing gradually away from rachidian. Marginal teeth numerous, with broad tips, edges finely and sharply serrate, serrations similar to those of laterals. Marginals and outer laterals with one long denticle on outer edge of shaft near overhanging tip.

Type locality: Snake Pit hydrothermal field, Mid-Atlantic Ridge (23°22'N, 47°57'W), 3,475 m.

Type material: Holotype and 20 paratypes from *Nautilite* dive HS10, 28 June 1988. Holotype MNHN; 16 paratypes MNHN; 2 paratypes LACM 2424, 2 paratypes

USNM 859485. The holotype is the only specimen in which both body and shell are in good condition, although the shell is heavily coated with mineral deposits. All other paratypes are smaller and completely decalcified so that they can not be measured. Bodies are mostly separated from the shell remnants and are somewhat mangled, although it is evident that the gonad protrudes on the left side in each. The radula was prepared from a detached body.

DISCUSSION

Pseudorimula midatlantica differs from *P. marianae* in having the right shell muscle longer than the left rather than having three separate muscles, a hypertrophied gonad that displaces the foot on the left side, a single pair rather than two pairs of anterior epipodial tentacles and two rather than four pairs of posterior epipodial tentacles. The two species can hardly be distinguished in shell profile or sculpture, although the holotype shell of *P. midatlantica* has an opaque interior, in contrast to the transparent condition in *P. marianae*. This, however, may be due to differences in preservation, including the treatment conditions that led to the decalcification of all paratype specimens of *P. midatlantica*.

In the original description of the genus *Pseudorimula*, I noted that the outer lateral teeth are morphologically similar to the inner marginal teeth, so much so that it is difficult to determine which are lateral teeth and which are marginal teeth. For *P. midatlantica* (figures 6, 7) I identify four pairs of lateral teeth by their more acute tips, compared to the broader terminations of the marginal teeth. Earlier (McLean, 1989: figs. 13C,D) I stated that *P. marianae* has five pairs of lateral teeth, but now revise that to four pairs based on re-examination of the original illustration.

Both of the two known species of *Pseudorimula* have differing features that set each apart from all other limpets: In *P. mariana* the shell muscle is inexplicably divided into three units, quite unlike the usual horseshoe-shaped muscle configuration in limpets of many families. In *P. midatlantica* the gonad is so hypertrophied that it displaces the foot on the left side; the shell muscle on the right side, where the foot remains large, is correspondingly longer. Which, then, of these two conditions is the more derived? We can assume that an ancestral species would have the usual horseshoe-shaped shell muscle and a gonad of normal size contained within the body cavity. Indeed, such a species may yet be discovered living on unexplored ridge systems. It is easy to understand the origin of the asymmetrical muscle pattern of *P. midatlantica* as an adjustment to gonad hypertrophication (in response to need for greater reproductive output) that eliminates space for muscle attachment on the left side, but there is no easy explanation for the presence of three separate shell muscles in *P. marianae*. If, however, the hypertrophied gonad of *P. midatlantica* were to revert to a normal size, the large right muscle would already be in place and the posterior muscle could

then be pinched off from the posterior tip of the right muscle, once there was no longer the need for a large right muscle.

The occurrence of the two species of *Pseudorimula* at such widely separate habitats as the Mariana Trough and the Mid-Atlantic Ridge is noteworthy but not unique. Martin and Hessler (1990) discussed "a growing body of evidence that there is a faunal connection between the Mariana vent area and the northern Mid-Atlantic Ridge." They mentioned similarities in the bythograeid crabs and gave three examples of genera represented in the two habitats, including *Pseudorimula* (as a personal communication from me), the shrimp genus *Chorocaris* (therein proposed), and a new genus of mussel (reported by Grassle, 1989). Martin and Hessler proposed that "the hydrothermal areas of the western Pacific and northern Mid-Atlantic Ridge were at one time connected via a series of active vent areas, not necessarily active simultaneously, that extended from the Mid-Atlantic Ridge south to the Atlantic-Indian Ocean Ridge, north along the Southwest Indian Ocean Ridge, Mid-Indian Ocean Ridge, and Southeast Indian Ocean Ridge, and finally north through the various spreading centers of the Indo-West Pacific."

Faunal connection between the Mariana Vents and those of the eastern Pacific were discussed by Hessler and Lonsdale (1991a,b). For vent limpets this applies only at the family level in the Clypeosectidae, as well as the Neomphalidae (McLean, 1990), but is exemplified at the species level by *Lepetodrilus elevatus* McLean, 1988, reported by McLean (1990) to occur at the Mariana vents as well as the east Pacific vents.

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Prodissoconch I and II Length in *Mercenaria* Taxa¹

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ABSTRACT

Mercenaria mercenaria larvae raised from 70 and 80 μm diameter eggs were reared for 48 hours, until the prodissoconch I boundary was clearly visible. Prodissoconch I lengths of larvae from 80 μm eggs were significantly greater than those from 70 μm eggs. Larvae from crosses using similarly sized eggs of *M. campechiensis* and *M. campechiensis texana* females and sperm from *M. campechiensis*, *M. campechiensis texana* and *M. mercenaria* males were reared through settlement. There were no significant differences in prodissoconch I lengths; however, prodissoconch II lengths of larvae sired by *M. mercenaria* were significantly longer than those sired by either subspecies of *M. campechiensis*. Differences in shell growth (ΔP = prodissoconch II – prodissoconch I length) also followed taxonomic lines.

Key words: Prodissoconch, egg, *Mercenaria mercenaria*, *Mercenaria campechiensis*, *Mercenaria campechiensis texana*.

INTRODUCTION

Relationships between egg size and shell length at the first shelled stage (i.e., prodissoconch I or protoconch I) have been reported for both bivalves and gastropods (Thorson, 1950; Robertson, 1971; Jablonski & Lutz, 1983; Lima & Lutz, 1990). Ockelmann (1962) suggested the usefulness of the length of prodissoconch I for estimating the egg size of bivalve species whose eggs were unavailable because of extinction or the inaccessibility of their habitat. Estimates of egg size could also be used to categorize the developmental strategy of a bivalve as lethic-trophic (150–200 μm diameter eggs), mixed (90–140 μm) or planktotrophic (40–85 μm) (Ockelmann, 1962). Smaller differences in the diameter of eggs ($\leq 50 \mu\text{m}$) within *Mercenaria* taxa and other planktotrophic species have been observed (Bricelj & Malouf, 1980; Barber & Blake, 1983; Heffernan *et al.*, 1989; Goodsell, 1991). Intraspecific differences in egg size have been attributed to the gametogenic state of the spawning female (Gallagher &

Mann, 1986). Small differences in egg size ($<10 \mu\text{m}$) may be reflected in the prodissoconch I length of *Mercenaria*, consequently allowing inferences from larval assemblages about the condition of the female parent and the survival potential of its eggs.

Developmental markers, such as prodissoconch I, remain visible with continued growth (figure 1) and their size can be compared to later shell features (e.g., prodissoconch II). In *Mercenaria* these shell markers delineate shell margin at the first shelled stage and at metamorphosis to a benthic existence. Although molluscan larvae have been shown to delay metamorphosis until suitable environmental conditions are found (Bayne, 1965; Crisp, 1974) no corresponding increase in shell length associated with the delay has been noted (Loosanoff, 1959).

Pechenik and Lima (1980) demonstrated an inverse correlation between growth rate and length of larval period of the common Atlantic slipper snail, *Crepidula fornicata* (Linnaeus, 1758). They hypothesized that length of larval life in the slipper snail is limited by the rate of development toward a “predetermined endpoint” and that such an endpoint might also exist in bivalves. Early studies by Loosanoff (1959) demonstrated that when the

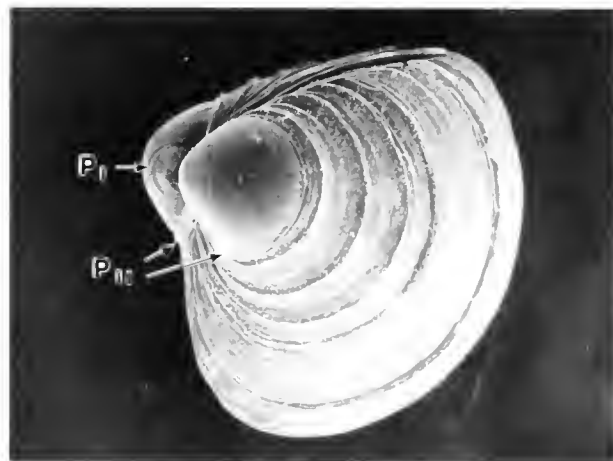


Figure 1. Scanning electron photomicrograph of a *M. campechiensis* juvenile 753 μm in shell length illustrating prodissoconch I (P I) and prodissoconch II (P II) boundaries.

¹ Technical contribution No. 3188 of South Carolina Experiment Station, Clemson University.

length of the larval period was increased by decreasing the culture temperature of *M. mercenaria* (Linnaeus, 1758) larvae there was no corresponding increase in shell length, supporting Pechenik and Lima's "endpoint" argument. The endpoint of larval bivalve life may be associated with the loss of feeding ability that occurs with the degeneration of the velum and ciliary feeding tracts (Bayne, 1965). Differences in prodissococonch II length may prove useful in detecting the difference in larval endpoints among *Mercenaria* taxa.

During the course of investigations into the genetics of *Mercenaria* we noted that eggs produced by any single, laboratory conditioned female during a given spawning event were remarkably consistent in diameter. The availability of these consistently sized eggs from known parents allowed us (1) to examine the relationship between egg diameter and prodissococonch I length in *M. mercenaria*; (2) to compare the prodissococonch I and II lengths of offspring from crosses involving *M. campechiensis* (Gmelin, 1791) and *M. campechiensis texana* (Dall, 1902) females with *M. campechiensis*, *M. campechiensis texana* and *M. mercenaria* males; and (3) to determine whether or not prodissococonch II lengths reflect taxonomic differences in parental stocks.

MATERIALS AND METHODS

Collection of adult *Mercenaria* and controlled spawning were achieved using methods previously described by Goodsell *et al.* (1992). Briefly, adults were collected from geographically isolated areas. *M. mercenaria* were collected from Milford, Connecticut; *M. campechiensis* from a site near Appalachicola, Florida; and *M. campechiensis texana* from a location near Galveston, Texas. Adults were conditioned at 19 °C for six weeks prior to spawning and were induced to spawn individually using thermal shock and the addition of pasteurized sperm. Eggs were counted (40×) and 100 eggs from each spawning female were measured with an ocular micrometer at 100× using a compound microscope. Eggs categorized as 70 µm had a minimum diameter of 70 µm, maximum diameter of 75 µm, mean <73 and standard deviation <2.0. Those categorized as 80 µm had a minimum diameter of 80 µm, maximum diameter of 85 µm, mean <83 and standard deviation <2.0. Sperm concentrations were estimated by spectrophotometry (Bricelj, 1979). To insure optimal gamete condition, all eggs were fertilized within one hour of spawning at the rate of 1,000 sperm ml⁻¹ (Goodsell, 1991).

EGG SIZE AND PRODISSOCOCONCH I LENGTH IN *M. MERCENARIA*

Fertilized 70 and 80 µm eggs of *M. mercenaria* were reared for 48 hours in 1 µm filtered, UV treated seawater at a density <20 eggs ml⁻¹. A mixed algal diet (25,000 cells ml⁻¹) was added to the culture at 24 hours. After 48 hours larvae were viewed with light microscopy (100×) to ensure that the prodissococonch I boundary was clearly

visible. Larvae were collected on a 44 µm mesh sieve and treated with sodium hypochlorite and distilled water to disarticulate the valves and remove soft tissues. Disarticulated valves from each species were mounted, shell margin downward, on double stick tape attached to a glass slide. Prodissococonch I lengths (n = 30) from each egg size category were measured with an ocular micrometer on a compound microscope (100×). Analysis of variance by general linear model was used to examine the effect of egg diameter on prodissococonch I length (SAS Institute, 1985).

PRODISSOCOCONCH I AND II LENGTH OF *MERCENARIA* TAXA

Larvae were reared for 15 days after prodissococonch I was achieved at a density of one larva ml⁻¹, to minimize the effects of crowding. Simultaneous spawning attempts resulted in crosses between female *M. campechiensis* (n = 3) and *M. campechiensis texana* (n = 2) and male *M. campechiensis* (n = 2), *M. campechiensis texana* (n = 1) and *M. mercenaria* (n = 3). No *M. mercenaria* females spawned during the trials. Egg diameters and prodissococonch I and II lengths were measured. Egg diameters (n = 100) from each spawning female were compared with an analysis of variance by general linear model to insure that egg sizes did not vary significantly between species. A measure of growth after the deposition of the prodissococonch I boundary was calculated for each larva (ΔP = prodissococonch II length - prodissococonch I length). Prodissococonch I and II lengths and ΔP for each parental cross were compared with analysis of variance by general linear model and differences among crosses were separated using least square difference (SAS Institute, 1985).

RESULTS

EGG DIAMETER AND PRODISSOCOCONCH I LENGTH IN *M. MERCENARIA*

Embryos derived from 80 µm eggs of *M. mercenaria* (mean = 80.9 µm, SE ± 0.32 µm) produce larvae with significantly greater ($P < 0.0001$) prodissococonch I lengths (109.7 µm ± 0.7; range 102–119) than prodissococonch I lengths (101.9 µm ± 0.7; 88–109) of those larvae derived from 70 µm eggs (70.8 µm ± 0.15).

PRODISSOCOCONCH I AND II LENGTH OF *MERCENARIA* TAXA

Prodissococonch I lengths from crosses using eggs of *M. campechiensis* and *M. campechiensis texana* (egg diameter = 75.4 µm ± 0.10) were not significantly different (table 1). However, significant differences ($P < 0.05$) in prodissococonch II length were found among the crosses. Metamorphosing larvae from crosses involving *M. mercenaria* males were significantly longer than from males of *M. campechiensis texana* and *M. campechiensis*. While

not statistically significant, it is interesting to note that the offspring of female *M. campechiensis* were longer than offspring of female *M. campechiensis texana*. No difference in prodissoconch II lengths of larvae from the male parents of the two *M. campechiensis* taxa was detected (Table 1). As expected, the growth (ΔP) differences among crosses were similar to those differences observed with the prodissoconch II lengths. Crosses involving male *M. mercenaria* demonstrated the greatest amount of shell growth.

DISCUSSION

Differences in prodissoconch I length was detected with differences in egg size as small as 10 μm in *M. mercenaria*; however, when similarly sized eggs were used no significant differences in prodissoconch I length were found among the closely related *Mercenaria* taxa. Prodissoconch I lengths appear to vary consistently with egg size probably from some minimum egg size. Gallagher and Mann (1986) suggested that a minimum threshold lipid level (= egg size) was necessary to achieve normal embryogenesis. Knowledge of the relationship between egg size and prodissoconch I length might provide a technique for predicting the threshold size of eggs produced by a female and the survival potential of its larvae.

Loosanoff (1959) observed that the shell lengths of metamorphosing *M. mercenaria* and *M. campechiensis* larvae from mass spawnings were similar, suggesting that these taxa shared a similar larval endpoint (Pechenik & Lima, 1980). In contrast with Loosanoff's (1959) earlier study, we found differences in the mean prodissoconch II length (= shell length at metamorphosis) among offspring sired by *M. mercenaria* and *M. campechiensis*. These differences in prodissoconch II length between the two species lend support to the placement of the *texana* subspecies within *M. campechiensis*. Examination of the distance between the prodissoconch I and II boundaries (ΔP) demonstrated that differences in prodissoconch II lengths were a function of growth differences among the taxa after the prodissoconch I boundary had been deposited. The sampling technique in our study was different from that of Loosanoff (1959). Loosanoff's (1959) results were based on mass spawnings with no attempt to limit the range of egg diameter. Furthermore, in Loosanoff's (1959) study, shell length at metamorphosis was determined by measuring the length of intact larvae as soon as they were observed to have lost their vela. In our study, shell length at metamorphosis was determined by measuring length at the prodissoconch II/dissoconch boundary on disarticulated values.

Prodissoconch I length does appear to be a good indicator of egg diameter. Also, prodissoconch II lengths (predetermined endpoint) follow taxonomic lines indicating genetic input as suggested by Pechenik and Lima (1980). Finally, prodissoconch I and II lengths should prove valuable in determining the condition of known parents and the relative genetic contributions of the parents in reciprocal crosses.

Table 1. Mean, standard error, range and results of least square difference test^a for prodissoconch I (P I) and II (P II) lengths (μm) and growth (ΔP), measured as prodissoconch II - prodissoconch I, by cross. Means not sharing the same letter are significantly different

Prodissoconch I length				
Cross ^b	n	P I \pm SE	Range	LSD Grouping
TC	100	104.1 \pm 0.34	91-107	A
TT	50	103.9 \pm 0.54	99-112	A
CT	75	103.7 \pm 0.47	91-116	A
TM	150	102.4 \pm 0.35	91-116	A
CM	225	101.8 \pm 0.29	91-116	A
CC	150	101.4 \pm 0.37	91-116	A
Prodissoconch II length				
Cross	n	P II \pm SE	Range	LSD Grouping
CM	225	260.0 \pm 0.91	224-290	A
TM	150	256.2 \pm 0.72	223-273	A B
CT	75	246.0 \pm 1.27	215-282	B C
TT	50	243.1 \pm 1.27	224-265	C
CC	150	243.0 \pm 0.87	215-273	C
TC	100	240.1 \pm 0.99	199-261	C
Growth (ΔP)				
Cross	n	$\Delta P \pm$ SE	Range	LSD Grouping
CM	225	158.3 \pm 0.89	124-191	A
TM	150	153.8 \pm 0.80	116-169	A B
CT	75	142.4 \pm 1.34	112-182	B C
CC	150	141.6 \pm 0.85	107-174	C
TT	50	139.2 \pm 1.24	124-165	C
TC	100	136.0 \pm 1.03	91-162	C

^a Alpha = 0.05, df = 8.

^b Abbreviations, *M. campechiensis* pure strain (CC), *M. campechiensis texana* pure strain (TT), hybrid from *M. campechiensis* female \times *M. mercenaria* male (CM), *M. campechiensis texana* female \times *M. mercenaria* male (TM), *M. campechiensis* female \times *M. campechiensis texana* male (CT), reciprocal hybrid (TC) in descending order of size

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Harpa cabriti Fischer, 1860, a replacement name for *Harpa ventricosa* Lamarck, 1816 (Gastropoda: Harpidae)

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ABSTRACT

Harpa ventricosa Lamarck, 1816, is preoccupied by *Harpa ventricosa* Lamarck, 1801, a name that is here determined to be an objective junior synonym of *Harpa major* Röding, 1798. The name *Harpa ventricosa* Lamarck, 1816, used for a western Indian Ocean species, should be replaced by *Harpa cabriti* Fischer, 1860, a name based on an immature specimen formerly considered a junior synonym of *Harpa ventricosa* Lamarck, 1816, non Lamarck, 1801.

Key words: Harpidae, *Harpa*, nomenclature.

In 1986 Richard E. Petit and I submitted an application to the International Commission of Zoological Nomenclature (ICZN) proposing that the specific name *Harpa articularis* Lamarck, 1822, be conserved and placed on the Official List of Specific Names in Zoology (Rehder & Petit, 1987).

When Miss Ruth A. Cooper of the ICZN was drafting the Opinion on this case she encountered a problem with our use of the name *Harpa ventricosa* Lamarck, 1816, noting that there was an earlier, validly published, *Harpa ventricosa* Lamarck, 1801 (Lamarck, 1801:79). That portion of the case involving *Harpa ventricosa* Lamarck,



Figure 1. Holotype of *Harpa cabriti* Fischer, 1860. BM(NH) 1899.8.22.126. No locality data. Scale bar = 3 cm.

1816, and *Harpa urniformis* Perry, 1811, was therefore withdrawn from the petition, being considered a purely taxonomic question, and Opinion 1518, conserving the specific name *Harpa articularis* Lamarek, 1822, was published in 1989.

Through a now inexplicable oversight I had overlooked, in my monograph of the family Harpidae (Rehder, 1973), the problem of homonymy involved in *Harpa ventricosa* Lamarek, 1801, versus *Harpa ventricosa* Lamarek, 1816. The present paper was written to clarify this matter.

In 1801 Lamarek published his "Système des Animaux sans Vertèbres", which in essence is a treatise on the classification of the invertebrates, listing the genera of the various groups, each genus being briefly diagnosed, with one or more species cited as examples. The species are without diagnoses but have bibliographic references to previous descriptions or figures.

His genus *Harpa* (Lamarek, 1801:79) is exemplified by one taxon, *Harpa ventricosa* Lamarek, a new name for the species illustrated by Lister (1770:pl. 992, fig. 55), and by Martini (1777:pl. 119, fig. 1090). Lister's figure represents *Harpa harpa* (Linné, 1758), as noted by Lamarek (1822:256) and Dodge (1956:196–198). Martini's figure is representative of *Harpa major* Röding, 1798, and was the figure on which Röding based his species. I therefore propose that the specimen illustrated in Martini's figure serve as the type specimen of *Harpa ventricosa* Lamarek, 1801. I did this in the case of Röding's name (Rehder, 1973:247). This makes Lamarek's name an objective junior synonym of *Harpa major* Röding, 1798.

Harpa ventricosa Lamarek, 1816, is a junior homonym but not a junior synonym of *Harpa ventricosa* Lamarek, 1801. Therefore, the species that had been called *Harpa ventricosa* Lamarek, 1816, by me (Rehder, 1973:251) and numerous other authors beginning with Lamarek (1822:255), is in need of a replacement name.

I therefore propose that this species, which is restricted to the western part of the Indian Ocean and the Red Sea, bear the name of *Harpa cabriti* Fischer, 1860. The type specimen of *H. cabriti*, which I listed in the synonymy of *Harpa ventricosa* Lamarek, 1816 (Rehder, 1973:252), is a juvenile or immature specimen, and is in

the collections of The Natural History Museum, London. Through the kindness of Ms. Kathy Way I am able to illustrate this holotype [BM(NH) 1899.8.22.126] (fig. 1).

Harpa urniformis Perry, 1811, although listed in the synonymy of *H. ventricosa* Lamarek by Deshayes (1843), is not identifiable and is not considered to be a senior synonym of *H. cabriti* Fischer.

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Obituary: Rae Baxter, 1929-91

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Alaskan malacology suffered a great loss with the death of Rae Baxter, the most knowledgeable expert on Alaskan mollusks, on 22 March 1991 at the age of 61. Rae was a Field Associate in Malacology of the Los Angeles County Museum of Natural History. He is survived by his wife Sera, daughter Lynx, and son Brant.

Rae was born on 30 March 1929 in Compton, California. He earned a Bachelor of Science degree in fisheries from Humboldt State University, California, in 1955. During his days at Humboldt, he became a student and collector of Pacific coast mollusks. While there he met Sera Miller, a native of Washington State, whom he married in 1955. Finding that northern climates were to their liking, Rae and Sera moved to Alaska after graduation.

From 1956 to 1962, Rae worked for the US Fish and Wildlife Service out of Anchorage. Winters during this period were spent camping and trapping, during which Rae and Sera learned much about cold weather survival techniques. In 1960, the Baxters spent five months traveling in their sport boat from Kachemak Bay through southeastern Alaska and British Columbia to the Stillaguamish River in Washington, camping on shore each night. Mollusks were collected at every opportunity and mailed back to Alaska. Sediment samples often were dried over the same stove used for cooking.

In 1962 Rae joined the Alaska Department of Fish and Game, being stationed first at Cordova. During this period the Baxters built an A-frame dwelling for use as a base for commercial salmon fishing at Kasitsna Bay, on the southern shore of Kachemak Bay in Lower Cook Inlet. Sera was in charge of this venture, which continued each summer, with the help of their children. In 1966 Rae was transferred to the Fish and Game laboratory at Bethel, on the Kuskokwim River in western Alaska. The family lived at Bethel during the off season, returning to Kasitsna Bay each summer, until 1983, when Rae retired and returned to Kasitsna Bay year round. In 1989 Rae finished building a laboratory for his new work as a marine biological consultant, and especially for research on his mollusk collection, for which he had assembled a good working library.

Although Rae's work for the state of Alaska concerned the commercially important fishes and invertebrates, his compelling interest was the systematics and distribution of the molluscan fauna of Alaska. Over many years of field work throughout Alaska, Rae became familiar with the mollusks of the entire state, including the land and freshwater species as well as marine species. He especially knew the molluscan fauna of Kachemak Bay and would often set out alone in an open skiff for intertidal collecting and dredging. His spare time that was not devoted to collecting and studying mollusks was spent examining collections and gathering distributional records on visits to the Los Angeles County Museum of Natural History and the US National Museum of Natural History. After his retirement, he spent many summers aboard research vessels on long cruises in the Bering Sea, Chukchi Sea, and Gulf of Alaska, working as a consultant to the National Marine Fisheries Service on Alaskan fishery assessment surveys. One of these cruises was aboard the Soviet ship *Novokotovsk* in the northwestern Bering Sea during the summer of 1990. Mollusks that would otherwise have been lost were retrieved by Rae on all the cruises.

At the time of his death he was completing a detailed key to the fishes of Alaska for publication by the American Fisheries Society. Upon completion of that project he was looking forward to being free to pursue his study of Alaskan mollusks, including the description of a number of species that he had recognized as new. He had started to construct specimen cases so that his collection, until then labeled with station numbers and species code numbers, could finally be assembled as a working reference collection. Rae's work on mollusks was not to be finished, but he has left a legacy both in his publications and his collection.

In 1983 Rae published the first edition of his distributional checklist, *The Mollusks of Alaska*, a major project that was greatly facilitated by the advent of personal computers, which enabled him to produce the finished text. Two subsequent editions (1985, 1987) were more detailed, treating a final total of 1,016 species. Two spe-



Rae Baxter at Kasitsna Bay, Alaska, in August 1973, screening mud dredged from his skiff (left) and picking salmon from a set net (right).

cies were described or coauthored by Baxter: *Macoma dexioptera* in 1977 and *Spiromoelleria kachemakensis* in 1984. Mollusks named in his honor were *Monadenia fidelis baxteriana* Talmadge, 1954, *Anatoma baxteri* McLean, 1984, and *Cocculina baxteri* McLean, 1986.

Rae was curious about all living things. He was a keen observer and was called upon for information by many biologists in Alaska. He often supplied live specimens for the aquaria at the Pratt Museum in Homer. He was always ready to assist the research of many workers around the world with specimens and information on Alaskan mollusks. Molluscan material from his field work in recent years was sent to the Los Angeles County Museum of Natural History, where it has greatly strengthened the Alaskan holdings. In accordance with his wishes, his entire mollusk collection has been transferred to the Los Angeles County Museum of Natural History, where it is to be integrated into the research collection and made available for study.

I was privileged to stay with the Baxter family at Kasitsna Bay for a week in August of 1973, a wonderful

experience both for the exposure to the rich molluscan fauna and the zeal with which Rae sought to understand it. Rae was a kind and generous man who is sorely missed.

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda, MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined, leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgements, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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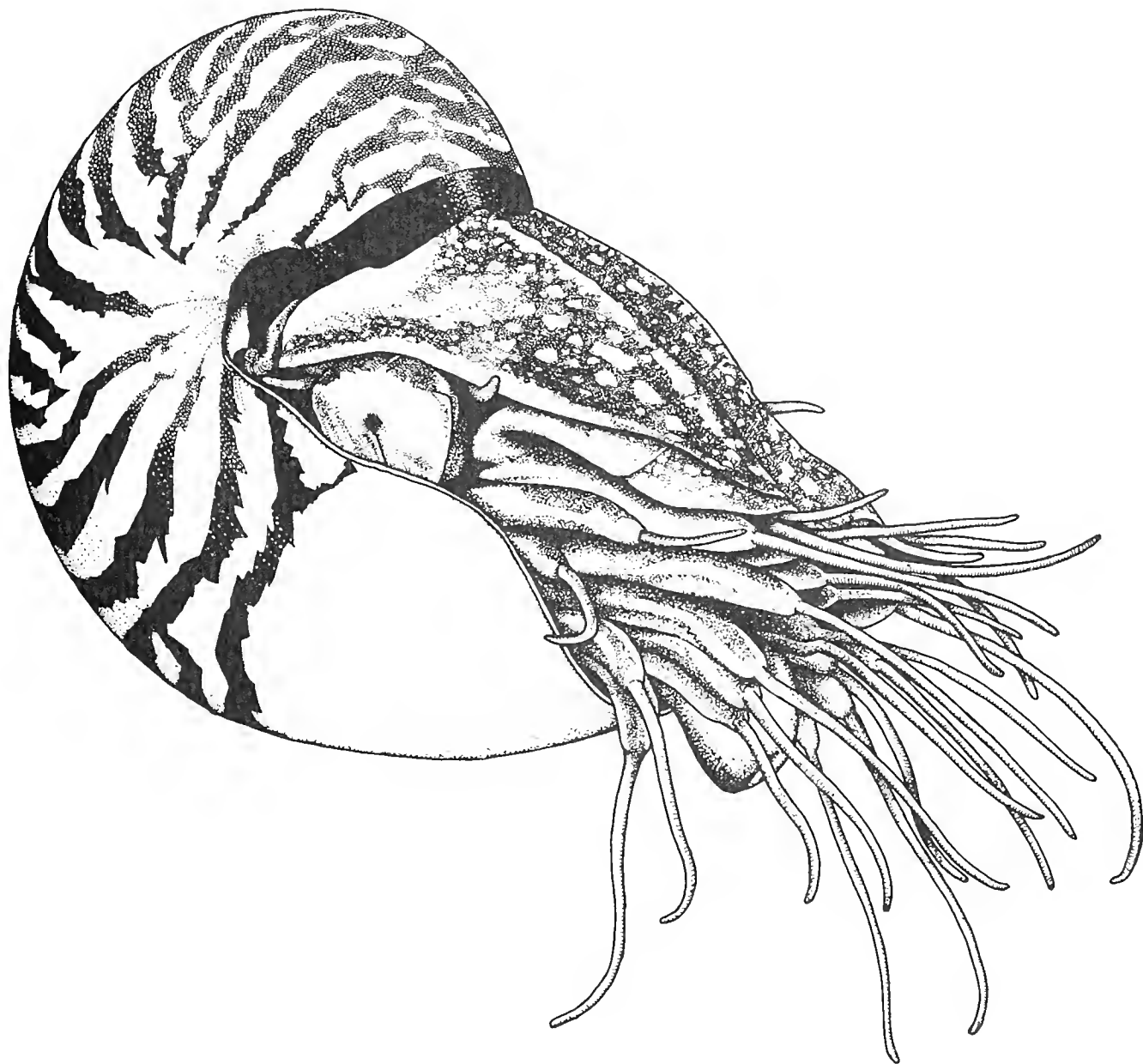
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Notice

SMITHSONIAN FUNDS FOR MALACOLOGY STUDENTS

The Division of Mollusks, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution announces the availability of the Rosewater Fellowship (up to \$750) to be awarded to graduate students of systematic malacology. This award provides support for students conducting systematic studies of Mollusca (leading to publication) who require access to collections and libraries of the Division of Mollusks, National Museum of Natural History. Funds can be used for travel, subsistence, and research costs. Interested students should submit a succinct proposal (1-2 pages), including budget with indication of any matching funds, and a supporting letter from faculty advisor(s). Application deadline is March 15, 1993. Award(s) will be announced on April 15, 1993. Applications should be sent to:

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A New Species of *Harpa* from the Leeward Islands of Hawaii

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ABSTRACT

Harpa goodwini, new species, is described from two localities in the Leeward Islands of Hawaii, French Frigate Shoals and Maro Reef, where it occurs in 82–228 m. This new species is most closely related to *Harpa cabritii* Fischer, 1860, once known as *H. ventricosa* Lamarck, 1816 (not Lamarck, 1801).

Key words: Gastropoda, Harpidae; *Harpa*; new species; Hawaiian Islands.

INTRODUCTION

On several occasions Mr. Donald Dan has turned over to me for study specimens of *Harpa* received by him from correspondents. One of these lots represents a striking new species from the Leeward Islands of the Hawaiian Group. I am grateful to Mr. Dan for the privilege of examining this material, and for permitting me to describe this new species.

ABBREVIATIONS FOR INSTITUTIONS

AMNH—American Museum of Natural History, New York
AMS—Australian Museum, Sydney
BM—Bernice P. Bishop Museum, Honolulu
BM(NH)—British Museum (Natural History), London
LACM—Los Angeles County Museum of Natural History, Los Angeles
MCZ—Museum of Comparative Zoology, Cambridge
MNHN—Muséum National d'Histoire Naturelle, Paris
MHNG—Muséum d'Histoire Naturelle, Geneva
NSMT—National Science Museum, Tokyo
USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC

SYSTEMATICS

Family Harpidae Bronn, 1849
Genus *Harpa* Röding, 1798
Harpa goodwini, new species
Figures 1,2; Table 1.

Description: Adult shell (figs. 1,2) 60–74 mm in length, broadly oval, outline of last whorl arcuate. Protoconch conical, pale pink, consisting of $2\frac{1}{4}$ to $3\frac{1}{2}$ convex, glossy whorls. Postnuclear whorls $3\frac{3}{4}$ –4 in number, first $1\frac{1}{2}$ whorls convex, pale pink in color, showing fine spiral cords at shoulder and below that cross fine axial riblets; this sculpture increasingly covered in subsequent whorls by the upper part of the glaze that covers the ventral wall at succeeding apertures and that extends up to the sharp spines of the axial ribs where they cross the shoulder cord. These spines become increasingly prominent and accentuate the flattened channel between suture and shoulder. On the upper whorls, the axial riblets in the channel are fine cords, but on the body whorl they become broader and flatter. Body whorl with 13–15 strong ribs that are erect with the moderately acute crest slanted away from the aperture along the apical half, but more rounded and flattened on the lower half of the rib. Ribs prominent and of orange color in the subsutural channel. At the shoulder, ribs form acute, triangular spines that are orange for most of the whorl, but become white near the aperture. The intercostal spaces are, as in most species of *Harpa*, axially finely striate.

Basic color of fresh specimens is pinkish to pinkish orange, with the spire whorls appearing yellowish due to the glaze covering. Ribs on the body whorl typically crossed by a series of eight pairs of dark chestnut lines that are generally more pronounced on the last four or five ribs and situated as follows: two pairs between the spine at the upper end of each rib and $\frac{1}{6}$ of the distance down the length of each rib; another two pairs along the center of the whorl; below that a single line (occasionally absent), then another pair of lines, and at the base three pairs of lines (the last may be obscure or appear as a single line), making a total of 17 lines. Between these four groups of lines are moderately broad bands composed of a central pale pink or orange pink band between two white bands. The intercostal spaces are marked with wavy, chestnut brown, axial lines, and, occasionally, by deep orange-rose splotches in two spiral bands, one in the center of the whorl, the other just below the spinose shoulder. Aperture oval with top of outer lip meeting the parietal wall at a right angle, the outer lip evenly

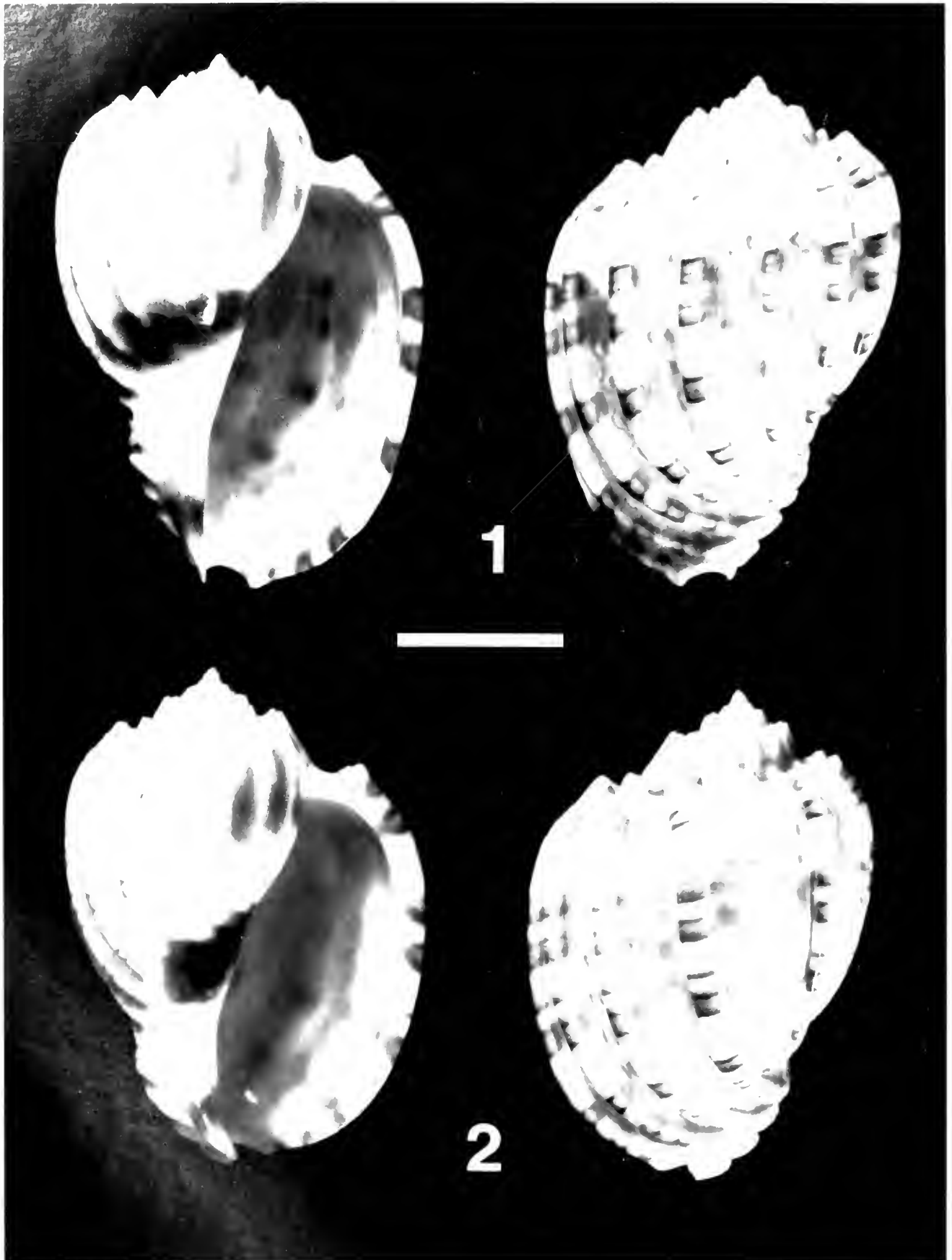


Table 1. *Harpa goodwini*, new species. Measurements of shell characters. Linear measurements in mm.

	Length	Width	No. ribs on body whorl	No. whorls	No. nuclear whorls
Holotype	63.8	45.1	15	7.00	3.33
Paratype 1	61.0	42.7	13	7.00	3.25
Paratype 2	73.4	57.3	14	6.00	2+
Paratype 3	74.8	55.2	14	6.16	2.33
Paratype 4	70.2	51.1	15	6.33	2.50
Paratype 5	70.3	52.5	15	6.25	2.50
Paratype 6	69.2	50.5	13	6.25	2.50
Paratype 7	70.4	48.1	15	6.33	2.50
Paratype 8	70.1	50.6	14	6.25	2.25
Paratype 9	66.2	44.7	15	6.12	2.12
Paratype 10	61.4	43.0	14	5.88	2.12
Paratype 11	60.4	43.7	15	6.00	2.25
Paratype 12	60.0	38.4	14	6.25	2.50
Mean	67.0	47.9	14.3	6.29	2.51
Range	60.0–74.8	38.4–57.3	13–15	5.88–7.00	2.12–3.33
SD	5.0	5.3	0.7	0.33	0.38

arcuate. Parietal wall of aperture gently convex, columella nearly straight, or slightly concave, anal fasciole strongly ridged by flattened ends of the ribs, the sinus fairly deep. Columella and parietal walls covered by a yellowish glaze, the outer lip yellow under the axial ribs, with deep chestnut lines on the ribs showing through as chestnut spots. The ventral wall has three chestnut spots: a strong, elongate central spot that slants apically into the aperture above the top of the columella; a weak, oval or roughly triangular spot between the ribs at the top of the parietal wall; and a small spot at the base of the columella.

Type locality: French Frigate Shoals, Hawaiian Islands, about 166°10'E, 23°45'N, 137 m. Taken with hermit crabs.

Material examined: Holotype, USNM 860312, Paratype 1, USNM 860314, from the type locality; Paratype 2, BM; Paratype 3, MCZ; Paratype 4, Goodwin Collection; Paratype 5, AMNH 226438; Paratype 6, BM(NH); Paratype 7, USNM 860315; Paratype 8, MHNG; Paratype 9, LACM; Paratype 10, AMS, Paratype 11, MNHN; Paratype 12, NSMT; all collected between French Frigate Shoals and Maro Reef, Hawaiian Islands, in 82–228 m.

Range: Leeward Islands, Hawaii, from French Frigate Shoals, to Maro (Dowsett) Reef.

Habitat: I am aware of only 13 specimens of this species having been collected, all from lobster traps set in depths ranging from 82 m to 228 m. All type specimens were brought into traps by hermit crabs.

Etymology: This new species is named after Daniel R. Goodwin of Honolulu, Hawaii, who collected all of the type specimens.

Comparative remarks: *Harpa goodwini* is a moderately large species characterized by its broad oval shape, its outline resembling that of *Harpa costata* (Linné, 1758) but with the outline of the last whorl more evenly arcuate, and differing by possessing an overall pinkish or orange-pink coloration when fresh, with dark horizontal stripes on the fewer, moderately broad and distant ribs. *Harpa major* Röding, 1798 differs from this new species in having a more oval shape, the whorls without the broad, flattened canal, and with the ribs fewer in number and lacking the dark horizontal lines.

This new species most closely resembles *H. cabritii* Fischer, 1860 (see Rehder, 1973:251–252; 1992:123), and has the same general arrangement of dark chestnut blotches on its ventral side. *Harpa goodwini* has, however, a relatively broader shell, with the body whorl not medially flattened but gently rounded. The axial ribs of *H. cabritii* lack the horizontal dark bands and numerous dark lines of *H. goodwini*.

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Figures 1, 2. *Harpa goodwini*, new species. 1. Holotype, USNM 860312. 2. Paratype 1, USNM 860313, both from French Frigate Shoals, Hawaiian Islands, about 166°10'E, 23°45'N, 137 m. Both specimens were brought into traps by hermit crabs. Scale bar = 2.0 cm.

Perotrochus maureri, a New Species of Pleurotomariid from the western Atlantic (Gastropoda: Pleurotomariidae)

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ABSTRACT

Perotrochus maureri, a new species of pleurotomariid, is described from the upper continental slope off northeastern Florida and the Carolinas. It can be distinguished from its sister species, *Perotrochus amabilis* (Bayer, 1963), and from the more remotely related *P. atlanticus* (Rios & Mathews, 1968) by its smaller, lower, more deeply pigmented shell with fewer spiral cords on the selenizone and shell base, as well as on the basis of its radular asymmetry and formula. The emergence of peninsular Florida is hypothesized to have separated the ancestral population into the Carolinian *P. maureri* and *P. amabilis*, which appears to be restricted to the Gulf of Mexico.

Key words: Pleurotomariidae; *Perotrochus*; new species; bathyal; vicariance; radula.

INTRODUCTION

During the course of continuing studies on the ecology and systematics of western Atlantic pleurotomariid gastropods, we had occasion to re-examine a large series of specimens that we collected off Charleston, South Carolina and previously referred to *Perotrochus amabilis* (Bayer, 1963) (Askew, 1988:91; Harasewych *et al.* 1988). Comparison of this material, as well as additional specimens from off Jacksonville, Florida, with the holotype and additional specimens of *P. amabilis* from off northern Cuba and throughout the Gulf of Mexico revealed subtle but consistent differences in size, pigmentation and sculpture. We ascribe these differences to allopatric speciation, and here describe as new the member of the species pair ranging from northern Florida to the Carolinas.

MATERIALS AND METHODS

The type material was collected during four dives aboard the Research Submersible NEKTON DELTA, in the area of the "Charleston Lumps," a region of rugged topography some 90 miles east of Charleston, South Carolina, on May 2–4, 1987. Some of the specimens were fixed in 10% sea

water formalin and stored in 70% ethanol for dissection; the remainder were frozen and maintained at -80°C .

Additional specimens of the new species, as well as comparative material of *P. amabilis* and *P. atlanticus* in museum collections were examined, and are identified in the text by the following institutional acronyms:

AMNH—American Museum of Natural History, New York

AMS—Australian Museum, Sydney

ANSP—Academy of Natural Sciences, Philadelphia

BM(NH)—British Museum (Natural History), London

FM—Fernbank Museum of Natural History, Atlanta

FMNH—Field Museum of Natural History, Chicago

FSBC I—Florida Marine Research Institute, St. Petersburg

HBOM—Harbor Branch Oceanographic Museum, Ft. Pierce, Florida

LACM—Los Angeles County Museum of Natural History

MCZ—Museum of Comparative Zoology, Cambridge

MNH—Muséum National d'Histoire Naturelle, Paris

USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC

SYSTEMATICS

Perotrochus maureri new species.

Synonymy:

Perotrochus amabilis: Askew, 1988:91; Harasewych *et al.* 1988. (Non *Perotrochus amabilis* (Bayer, 1963)).

Description: Shell (fig. 1) medium-sized (to 52 mm), thin, trochoid, non-umbilicate, of up to $9\frac{3}{4}$ whorls. Spire coelocoonoid, straight for first 5 whorls, becoming increasingly concave thereafter. Protoconch (figs. 2–3), 500 μm wide, of 1 smooth, glossy, translucent whorl. Transition to teleoconch abrupt, delimited by slightly flared protoconch lip, onset of spiral and axial sculpture, selenizone. Selenizone initially nearly abutting suture, descending to mid-whorl by whorl 2, below mid-whorl by whorl 6. Axial sculpture of pronounced prosocvrt riblets

Table 1. Measurements of shell characters in *Perotrochus maureri*, *P. amabilis* and *P. atlanticus*. Linear measurements in mm

Character	<i>Perotrochus maureri</i> (n = 10)			<i>P. amabilis</i> (n = 8)			<i>P. atlanticus</i> (n = 3)		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Maximum diameter (MD)	46.1	34.4–59.5	6.6	72.2	44.9–87.2	12.1	57.0	56.3–58.2	0.9
Shell height (SH)	37.3	34.7–46.9	4.1	60.58	41.7–73.3	6.1	53.7	52.7–54.8	0.9
SH/MD	0.822	.791–.832	0.01	0.855	.840–.929	0.03	0.940	.936–.951	0.00
No. whorls, teleoconch	8.78	8.25–9.75	0.37	9.76	9.0–10.75	0.54	9.33	9.0–9.75	0.31
No. spiral cords on selenizone	1.80	1–3	0.75	2.88	2–4	0.60	3.33	3–4	0.47
No. spiral cords on shell base	19.0	16–22	1.6	28.2	24–31	2.3	27.0	23–31	3.3

(18–20 on whorl 1), above and below selenizone, aligned in early whorls. Riblets decrease in prominence, being reduced to beads on spiral cords by whorl 6. Spiral sculpture initially of fine threads that cross riblets at angle (20–30°) to converge on selenizone from above and below. Single, continuous spiral cord first appears above the selenizone on whorl 2, below the selenizone on whorl 4. Selenizone with opisthocyrt ribs that are more numerous than, and unaligned with, prosocyrt ribs. Spiral sculpture on selenizone of fine radial threads between adjacent ribs on early whorls, single medial spiral cord by whorl 4. Number of spiral cords above/on/ below the selenizone increasing to 3–4/1/2–3 on whorl 6, 6–8/1–3/3–4 on whorl 8. Suture initially grooved, becoming flat by whorl 5, impressed by whorl 7. Aperture horizontally ovately-rhomboidal. Outer lip smooth, portion below slit offset from portion above slit by 30–33°. Slit narrow, extending posteriorly 84–92° from outer lip. Columella spirally coiled, with strong sigmoid flexure near adapical margin. Umbilical region excavate but not perforate. Base convex, with 17–22 even spiral cords between periphery and umbilical region, which is nacreous due to resorption of outer layers of shell. Base color ivory, with broad axial bands of pale brick red, and narrower bands of dark red. Aperture nacreous, iridescent. Operculum (fig. 4) small, (spanning 0.6 of minor axis of aperture) multispiral, corneous.

Anatomy: As the anatomy of *P. maureri* agrees in most regards with that of *P. amabilis* as described by Fretter (1964); only supplemental observations on living animals are recorded. The foot, head and tentacles are densely mottled with dark brick red. When the animal is crawling, the posterior portion of the shell is supported on the operculum. Tentacles are long, cylindrical, ventrally directed. Left tentacle bilobed in one of the five specimens dissected. The jaws, inner lips and outer lips are all interconnected, being formed of a single piece of scleroprotein. The heavily papillated mantle edges on either side of the slit abut, sealing the slit except for a small opening along the posterior 1/5 of its length. The ctenidia do not project beyond the mantle edge in living speci-

mens. When the animal is disturbed, the hypobranchial gland rapidly secretes large volumes of a whitish fluid that is immiscible with and denser than seawater. This secretion settles around and adheres to the shell.

Radula: Radulae of 5 specimens (39–52 mm maximum diameter) were examined. Radula (figs. 5–10, table 2) long (75–82% maximum shell diameter), asymmetrical, left-skewed, bifid posteriorly, composed of 92–104 inverted V-shaped rows of teeth. Hickman's (1984) terminology for the six tooth types is used herein and correlated to other terminologies in table 2. Rachidian Tooth (figs. 6, 8) with dorsal surface laterally expanded, forming flanges that apparently serve to maintain alignment between lateral teeth. Two long, Inner Lateral Teeth, with laterally expanded dorsal surfaces and broad, strongly curved distal ends (fig. 8, arrows) flank the rachidian tooth on each side. Adjacent are 24–26 (number increasing with shell size) Outer Lateral Teeth (figs. 6–8) that are shortest opposite Inner Lateral Teeth of adjacent row (fig. 7), and become progressively broader and stouter, with the long axis of the basal plates of the outermost Outer Lateral Teeth nearly perpendicular ($\approx 70^\circ$) to that of the innermost Outer Lateral Teeth and to the radular axis (fig. 8). These in turn are flanked by 21 large, curved Sickle Teeth (figs. 5–7). As in *P. amabilis*, the innermost teeth are tricuspid (fig. 7, arrow), but the cusp on the concave surface is lost in subsequent teeth (Fretter, 1964: 181). The transition from Sickle Teeth to Filament-Tipped Teeth is gradual, the first Filament-Tipped Tooth discerned by the presence of two minute bristles on either side of the proximal cusp (Woodward, 1901:250). The bristles increase in number and become larger, while the cusps diminish in size (fig. 9) and ultimately are lost in the outermost Filament-Tipped teeth. The outermost 8–9 teeth (fig. 10), referred to as Paddle-Shaped Teeth, are broad, flat, and blunt ended, the preceding 1–2 teeth are transitional from Filament-Tipped teeth to Paddle-Shaped Teeth and retain vestiges of a filaments along the inner distal ends. The Paddle-Shaped Teeth of one row overlap the outer Filament-Tipped Teeth of the adjacent, more proximal row, forming a telescoping mar-

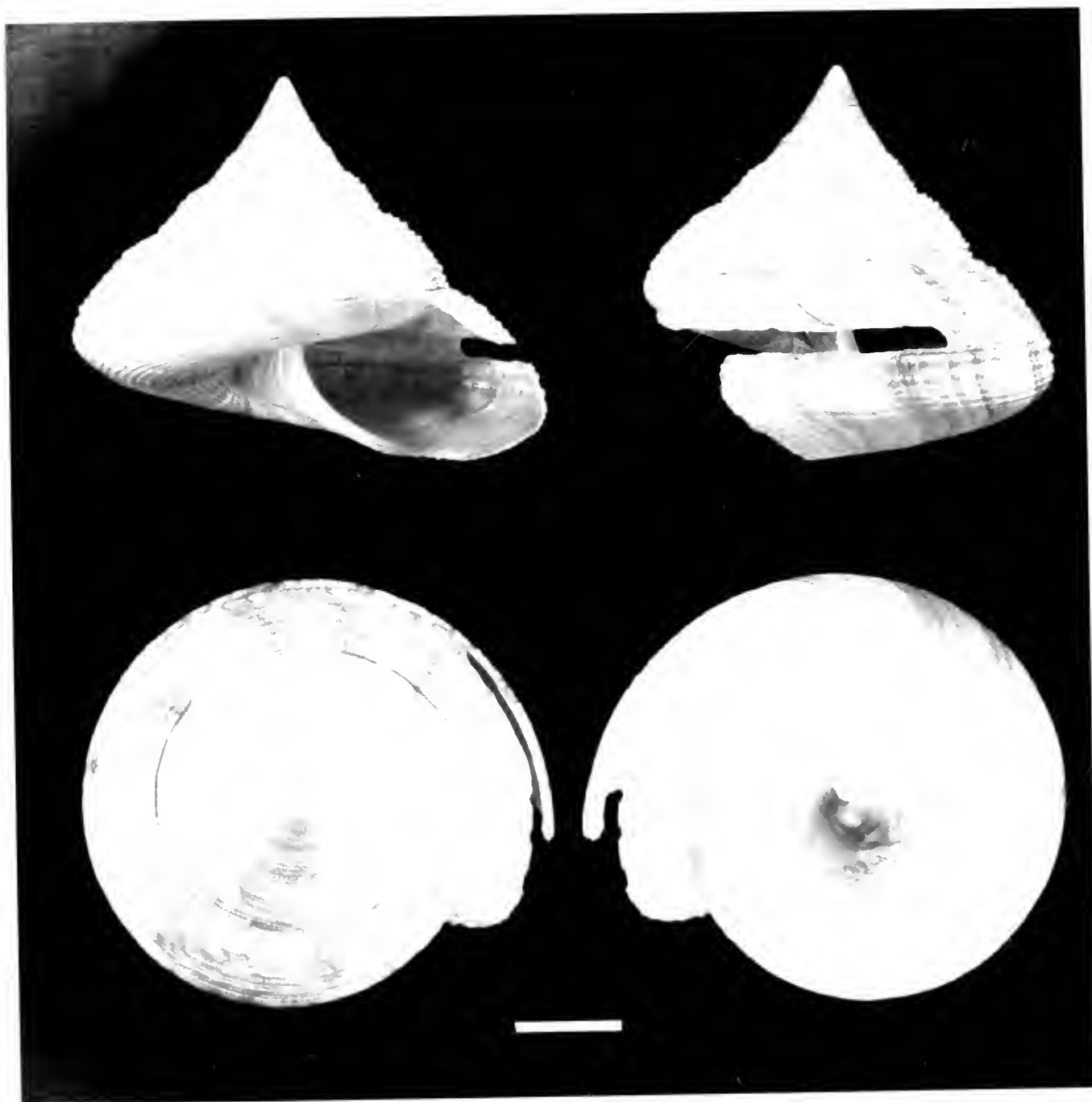


Figure 1. *Perotrochus maurei*, new species. Apertural, lateral, ventral and dorsal views of holotype (USNM 860320). Off Charleston, South Carolina, USA, (32°43'57"N, 78°05'41"W) in 195–204 m. Scale bar = 1.0 cm.

gm that envelops the Filament-Tipped Teeth and facilitates smooth motion of the radula within its sheath on the rasping stroke. The blunt ends of the Paddle-Shaped Teeth may also dislodge entangled sponge tissue and spicules from the radula and free them to pass into the esophagus.

Type locality: 90 nautical miles E of Charleston, South Carolina, USA, (32°43'54"N, 78°06'00"W) to (32°44'02"N, 78°05'22"W) in 195–213 m.

Range: *Perotrochus maurei* occurs on the upper continental shelf off Charleston, South Carolina and Jacksonville, Florida, in depths of 193–366 m.

Type specimens: Holotype, USNM 860320. Paratypes 1–9, USNM 875218, Paratype 10, AMS C 169400, Paratype 11, BMNH, Paratype 12, MNHN, Paratype 13, FMNH, Paratype 14, ESBC I, all from R/V NEKTON DEPTA dive 561, (32°43'57"N, 78°05'41"W) in 195–204 m, 4 May 1987. Paratypes 15–17, LACM 2629, Paratype

Table 2. Comparison of formulae and asymmetries of pleurotomariid radula. Sources of data footnoted. ? indicates that the character could not be inferred from cited text or figure.

Taxon	N	A: Rachid- ian	Lateral teeth		Marginal teeth			Skew*
		B: Rachid- ian	Central	Lamellate	Hooked	Brush	Flabelliform	
		C: Rachid- ian	Inner laterals	Outer laterals	Sicle	Filament- tipped	Paddle- shaped	
<i>Mikadotrochus beyrichi</i> ¹	4 ²	1	3	20–21	17–22	63–65	7–12	R ¹
<i>Perotrochus quoyanus</i> ²	1 ²	1	3	24	13	63	6	R ^{9,10}
<i>P. caldedonicus</i> ³	1	1	1	22	14	53	7	R ¹¹
<i>P. notialis</i> ⁴	1	1	2	29	13	63	10	?
<i>P. amabilis</i> ⁵	1	1	3	24	21	63	8	R ¹²
<i>P. maureri</i> ⁶	5	1	2	24–26	21	61–63	8–9	L ⁶
<i>P. midas</i> ⁷	1	1	3	26	13	63	6	L ^{9,10}
<i>P. lucaya</i> ⁷	1	1	3	25	13	61	6	?
<i>P. africana</i> ⁸	1	1	4	25	12	50	6	?

A = Standard terminology (e.g., Fretter & Graham, 1962:169). B = Terminology of Woodward, 1901, and other authors. C = Terminology of Hickman, 1984.

* R = Right-skewed asymmetry. L = Left-skewed asymmetry.

¹ The radular formula given by Woodward (1901:252) and subsequently cited by other authors, is an incorrect summation of the data contained in his paper. His report that there are 223 teeth per row (p. 247), and explicit statement that there are 21 lamellate teeth (p. 249) indicate that the correct radular formula is (R-3-21-17-63-7), at least for the three specimens that he examined. Bouvier and Fischer (1902) report a radular formula of (R-3-20-22-65-12) for this species.

² Bouvier and Fischer, 1899.

³ Rouchet and Metivier, 1982:310.

⁴ Leine and Penna, 1969:227.

⁵ Fretter, 1964:181.

⁶ Herein.

⁷ Fretter, 1966:608.

⁸ Barnard, 1963:157. Listed as approximate counts.

⁹ Hickman, 1981:190.

¹⁰ Hickman, 1984:30.

¹¹ Rouchet and Metivier, 1982:fig. 2.

¹² Herein, n = 2.

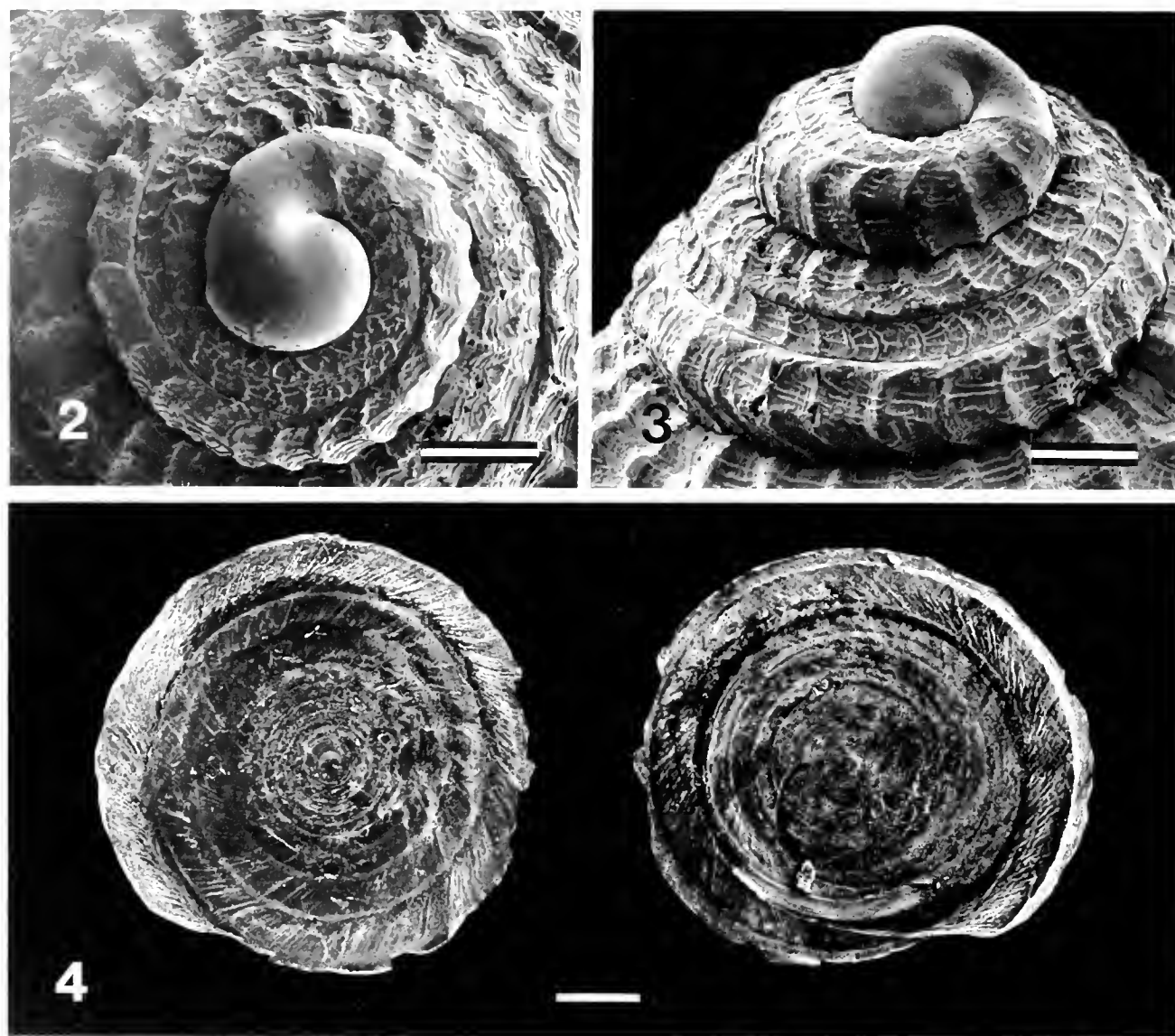
18–20, USNM 875221, Paratype 21, MCZ, Paratype 22, ANSP, Paratype 23, AMNH, R/V NEKTON DELTA dive 557 (32°43'54"N, 78°06'00"W) in 198–213 m, 2 May 1987. Paratypes 24–26, USNM 846900 (reported in Harasewych *et al.* 1988:94 as *Perotrochus amabilis*), R/V NEKTON DELTA Dive 560, (32°43'58"N, 78°05'43"W) in 198–210 m, 3 May 1987. Paratypes 27–33, USNM 860321, Paratypes 34–35, FM 92.15. 1–2, R/V NEKTON DELTA Dive 562 (32°44'02"N, 78°05'22"W) in 204–213 m, 4 May 1987. Paratype 36, HBOM 65:1985 JOHNSON-SEA-LINK-1-1455, about 80 n miles off Charleston, South Carolina, USA 32°44.0'N, 78°05.6'W, in heavy rubble zone of rocks and sand, 193 m. September 6, 1983.

Other material examined: HBOM 65:2017 Off Charleston, SC circa 1982; AMNH 226434, AMNH 226435, AMNH 226436, and USNM 869531, all from Off Jacksonville, Florida, in 366 m.

Comparative material examined: *Perotrochus amabilis* (F.M. Bayer, 1963): Holotype USNM 635625, S.E. of Sombrero Light, Florida (24°29'N, 80°53'W–24°30'N, 80°50'W), trawled in 220 m, R/V GERDA Cruise 6333, haul G-135; USNM 801707, 100 miles NNE of Sagua La Grande, Cuba (23°35'N, 79°34'W), in 183–238 m, R/V

SILVER BAY sta. 2460; USNM 846648, W of Tampa, Florida, rubble bottom, 210 m; USNM 858215, Green Canyon, 100 miles S of Atchafalaya Bay, Louisiana (27°44'35"N, 91°07'54"W), in 170 m, JOHNSON-SEA-LINK-1-2385, 17.6°C; AMNH 183151, WNW of Ft. Myers, Florida, in 220 m; AMNH 244316, Dry Tortugas, Florida (no depth); FSBC I 30812, About 97 nautical miles W. of Mullet Key, Pinellas County, Florida (27°39'N, 84°33'W), in 126.2–128.0 m. R/V HERNAN CORTEZ; FSBC I 33146, About 95 nautical miles W. of Anna Maria Island, Manatee County, Florida (27°31'N, 84°31'W) in 135.6–126.5 m. R/V HERNAN CORTEZ; HBOM 65:02190, About 100 nautical miles SE of Galveston, Texas, in 268.2 m. JOHNSON-SEA-LINK-II-933. *Perotrochus atlanticus* (Rios & Mathews, 1968): USNM 846647, Off Rio Grande, Rio Grande do Sul, Brazil, in 260 m; AMNH 181294, Off Rio Grande, Rio Grande do Sul, Brazil, in 164 m, sand & mud; AMNH 244317, Solidao, Brazil.

Ecology: Specimens were observed *in situ* at the type locality, an area of rugged terrain consisting of steep, large (3–30 m) hill crests and valleys. *Perotrochus maureri* was largely confined to hard substrates, composed of slabs or fragments of relithified phosphorite, that lined



Figures 2-4. *Peretrochus maureri*, new species. 2. Apical and 3. oblique views of protoconch. Scale bars = 250 μ m. 4. Outer and inner views of operculum. Scale bar = 1.0 mm.

the tops and sides of the hill crests (see Askew, 1988:90, fig. 2). Water temperature was 9.6-9.8°C. *Peretrochus maureri* occurs in considerable densities at the type locality, with distances between specimens ranging from 10 to 30 meters. The diet of *P. maureri* [as *P. amabilis*] was reported by Harasewych *et. al.*, (1988) to consist on sponges of the orders Poccilosclerida, Choristida or Spirophorida, and the genus *Strongylophora*. Most speci-

mens have 7-12 repaired shell breaks, indicating frequent, unsuccessful predation, probably by crustaceans.

Etymology: This species is named in honor of Mr. Richard S. Maurer in recognition of his long and devoted interest in, and support of Malacology.

Discussion: *Peretrochus maureri* is most closely related to *P. amabilis*, and more remotely related to *P.atlan-*

Figures 5-10. Radular ribbon of *Peretrochus maureri*. 5. Dorsal view of critical-point dried buccal mass, showing alternating arrangement of hooked teeth. Scale bar = 500 μ m. 6. Anterior view of extended, critical-point dried radula. Radula is seen to be asymmetrical and left-skewed. Scale bar = 500 μ m. 7. Left side of radula. Scale bar = 500 μ m. 8. Rachidian, inner and outer lateral teeth. Teeth to the left of the rachidian are further anterior than their homologues on the right. Scale bar = 250 μ m. 9. Filament-tipped teeth from two adjacent rows. Scale bar = 100 μ m. 10. Paddle-shaped teeth. Transition from filament-tipped to paddle-shaped teeth discernible on teeth 9-10 (arrows). Scale bar = 250 μ m.

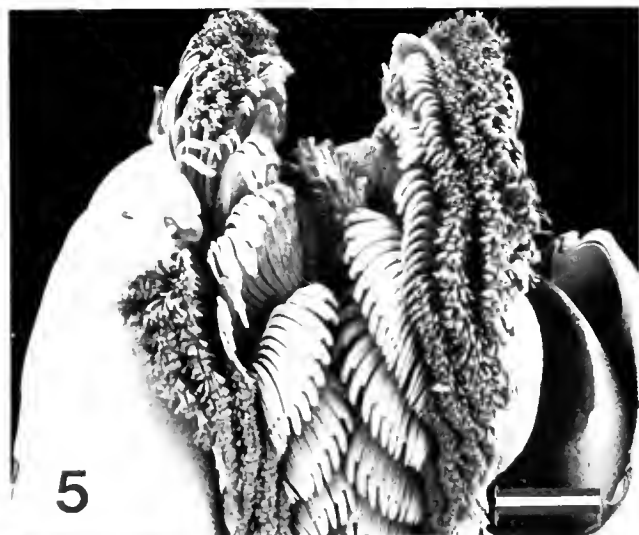




Figure 11. Map showing distribution of *Perotrochus amabilis* (Bayer) (dots) and *P. maureri* n. sp. (open circles). Solid and open stars denote respective type localities.

ticus. It can be distinguished from both these species by its smaller size, lower spire, and its more darkly pigmented shell with fewer spiral cords on the selenizone and base (Table 1). The radula of *P. maureri* differs from that of *P. amabilis* in being left-skewed rather than right-skewed, and in having one fewer Inner lateral Teeth, an equal or greater number of Outer Lateral Teeth, an equal or lesser number of Filament-tipped Teeth and an equal or greater number of Paddle-shaped Teeth (Table 2). The utility of minor differences in radular formulae for distinguishing taxa is questionable, as most reports to date are based on a single radula per species. Intraspecific variation in the numbers of Outer Lateral, Sickie, Filament-tipped and Paddle-shaped teeth has been encountered when multiple radulae have been examined (Table 2). As the transitions between the types of teeth are gradual (especially in the Marginal Teeth), it is also possible that different investigators may have assigned one or more transitional teeth to different tooth types, thus further obscuring the discriminating value of radular formulae. Radular asymmetry, however, appears to be constant within a species (*P. maureri*, left-skewed, $n = 5$; *P. amabilis*, right-skewed, $n = 2$), and is tentatively regarded as a useful distinguishing criterion.

Perotrochus maureri is known only from the upper continental slope off northeastern Florida and the Carolinas, where it occurs below the 10°C thermocline. Its sister species, *P. amabilis*, is limited to the Gulf of Mexico and the Straits of Florida (Fig. 11). A single temperature record from Louisiana (17.6°C) indicates that this species lives substantially above the 10°C thermocline. We surmise that the emergence of peninsular Florida separated the ancestral population during the Neogene, with *P. amabilis* evolving in the Gulf of Mexico, while *P. maureri* was isolated on limited areas of hard substrate off the Carolinas, and subsequently adapted to colder temperatures.

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The Genus *Fulgoraria* (Gastropoda: Volutidae) of the northeastern Kamchatka Peninsula and Sakhalin Island, with Notes on the Paleoecology and Distribution of the Subfamily Fulgorariinae in the Oligocene of the northern Pacific

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ABSTRACT

Four new species of the genus *Fulgoraria* Schumacher, 1817, (subgenus *Musashia* Hayashi, 1960) are described from the Oligocene Alugian Formation of the Ilpinsky Peninsula, northeastern Kamchatka Peninsula, Russia. Previously described fulgorariine gastropods from the same region, and from the Oligocene of Sakhalin and Karaginsky Islands, are also figured. Oxygen isotopic analyses of contemporaneous *Cyclocardia* shells, along with a comparison of the ecology of Recent congeneric taxa and a paleoecologic analysis suggest a bathyal environment as most probable for these Oligocene Fulgorariinae. A review of the Oligocene biogeography of northern fulgorariines along the northern Pacific margin, including the western coast of North America, indicates that this subfamily had a much broader distribution during late Paleogene time than today. These data point to more favorable climatic conditions (including lower water temperatures) for dispersal of fulgorariine volutes during the Oligocene.

Key words: Fulgorariinae; systematics; distribution; Oligocene; Paleogene; Northern Pacific.

INTRODUCTION

Volutid gastropods are common as fossils in Cenozoic faunas of the northern Pacific region. However, their fossil record from some parts of this region, particularly the far east of Russia, is still very incompletely known. The subfamily Fulgorariinae Pilsbry and Olsson, 1954, is the dominant group among North Pacific Cenozoic volutes. Recent members of the "northern group" (Shikama, 1967) of this subfamily are restricted to Japan and adjacent seas. Less well-known extinct species occurred along both eastern and western margins of the North Pacific during both early and late Cenozoic time.

The subfamily Fulgorariinae comprises a group of carnivorous gastropods with a uniserial radula composed of tricuspid rachidian teeth (Cooke, 1922; Habe, 1943; Okutani, 1963; Weaver & du Pont, 1970; Watanabe & Habe, 1978). The higher systematics of this subfamily is still not fully resolved, with the two most recent revisions (Shikama, 1967; Weaver & du Pont, 1970) differing primarily in the ranking of supraspecific taxa. Shikama (1967) recognizes three genera: *Fulgoraria* Schumacher, 1817, *Musashia* Hayashi, 1960, and *Saotomea* Habe, 1943, as well as the subgenera *Psephaca* Crosse, 1871, *Nipponomelon* Shikama, 1967, *Neopsephaca* Takeda, 1953, and *Mioleione* Dall, 1907. The last two are known only as fossils. Shikama's classification is based exclusively on shell characters such as the number and shape of columellar plaits, the size and form of the protoconch, and features of the external shell morphology. All of these characters, especially the number of columellar plaits, may vary during ontogeny. Interpreting this highly variable shell morphology is further complicated when working with fossil specimens, as they are often incompletely preserved.

Based on shell and radular characters, Weaver and du Pont (1970) recognized only a single Recent north Pacific genus *Fulgoraria*, with the subgenera *Psephaca*, *Volutipisma* Rehder, 1969, *Musashia*, *Kurodina* Rehder, 1969 and *Saotomea*. These authors regard *Nipponomelon* as a synonym of *Musashia*, and do not discuss the taxonomic position of the fossil *Neopsephaca* and *Mioleione*.

The present paper provisionally follows the classification of Weaver and du Pont (1970), but includes *Nipponomelon*, *Mioleione*, and *Neopsephaca* as subgenera of *Fulgoraria*.

Twenty-six species of Fulgorariinae from the latest Eocene and Oligocene formations of the north Pacific have been figured or described. Of these, eight are known only from North America [Poul Creek and Narrow Cape (of Sitkinak Island) Formations of Alaska; Blakeley, Twin River, and Eugene Formations of Oregon and Washing-

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ton], and have been referred to the subgenera *Nipponomelon*, *Musashia*, *Miolepleiona*, and *Neopsephaea* (Durham, 1944; Addicott *et al.*, 1971; Tegland, 1933; Allison & Marincovich, 1981; Moore, 1984). Nine species, referred to the subgenera *Fulgoraria*, *Psephaea*, *Musashia*, *Nipponomelon*, and *Neopsephaea*, are restricted to the Oligocene of Japan (Ashiya, Kishima, Nishisonogi, Kumano, and Chikokubo Formations of Kyushu and Honshu Islands; Momijiyama Formation of Hokkaido) (Oyama *et al.*, 1964; Shikama, 1967; Masuda & Noda, 1976). An additional seven species, from various localities along the northwestern coast of the United States and the Kamchatka Peninsula, have only been identified to the subgeneric level (Allison & Marincovich, 1981; Moore, 1984; Gladenkov, Sinelnikova & Bratseva, 1987). Only one species endemic to the Kamchatka Peninsula and the Koryak Upland, *Fulgoraria (Musashia) olutorskiensis* L. Krishtofovich, 1973, has been described to date. A second Siberian species, *Fulgoraria (Nipponomelon) tokunagai* (Kanehara, 1937) is more widespread and is also known from the Oligocene of Japan.

MATERIALS AND METHODS

All specimens in this study were collected during field work in eastern Kamchatka and Sakhalin Island between 1965 and 1986. They were taken from the Alugian Formation of northeastern Kamchatka, the "*Laternula*" sandstones of Karaginsky Island, and the Matchigarian Formation of central Sakhalin (fig. 21). The preservation of the specimens was often fragmentary, with the figured specimens representing the most complete material.

In order to address the questions of the ecology of these Oligocene fulgorariines, a paleotemperature analysis of shells of *Cyclocardia ilpinensis* Pronina, 1973, which occurs in abundance in the same strata as the volutes, was conducted. This standard analysis was based on the ratio of the oxygen isotopes (^{18}O : ^{16}O). The values of ^{18}O : ^{16}O (PDB standard, mass spectrograph) were adjusted to the Standard Mean Ocean Water (SMOW) standard and corrected for altered isotopic composition at higher latitudes. Temperature values were calculated using the following formula:

$$T = 16.5 - 4.3(b - A) + 0.14(b - A)^2,$$

where T is the temperature in °C, b is the instrumentally determined difference in the ^{18}O : ^{16}O ratio between the sample and the standard, and A is the correction for the original isotopic composition of sea water. For high latitudes $A = -1$. Prior to analysis, all shells were examined using X-ray diffraction analysis to exclude specimens in which the aragonitic structure had recrystallized.

The following institutional acronyms are used: GI—Geological Institute, Russian Academy of Sciences, Moscow; CMG—Central Museum of Geology, St. Petersburg, Russia; USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

SYSTEMATICS

Family Volutidae Rafinesque, 1815
Subfamily Fulgorariinae Pilsbry and Olsson, 1954
Genus *Fulgoraria* Schumacher, 1817
Subgenus *Musashia* Hayashi, 1960

Fulgoraria (Musashia) novoilpinica new species
Figures 1, 2, 17

Description: Shell fusiform, slender, with 4–5 postnuclear whorls. Last whorl stout, comprising $\frac{2}{3}$ of shell height. Suture moderately impressed, subsutural band absent. Aperture elliptical (Length: width ≈ 3). Inner lip with one narrow columellar fold and siphonal fold. Siphonal canal wide. Axial sculpture of numerous (10–12 on penultimate whorl) thin ribs, more pronounced on earlier whorls, smoother and wider on body whorl. Spiral sculpture of fine, raised threads covering entire surface.

Material examined: Holotype—USNM 468649, length (incomplete) 119.5 mm, width 58.3 mm; Paratype—GI 4072, length (shell strongly decorticated) 124.7 mm, width 62.2 mm; 1 juvenile shell, 7 broken shells and fragments, 2 molds; all from the type locality.

Type locality: Northwestern part of the Ilpinsky Peninsula, eastern Kamchatka, Russia. Upper part of the Alugian Formation, Oligocene.

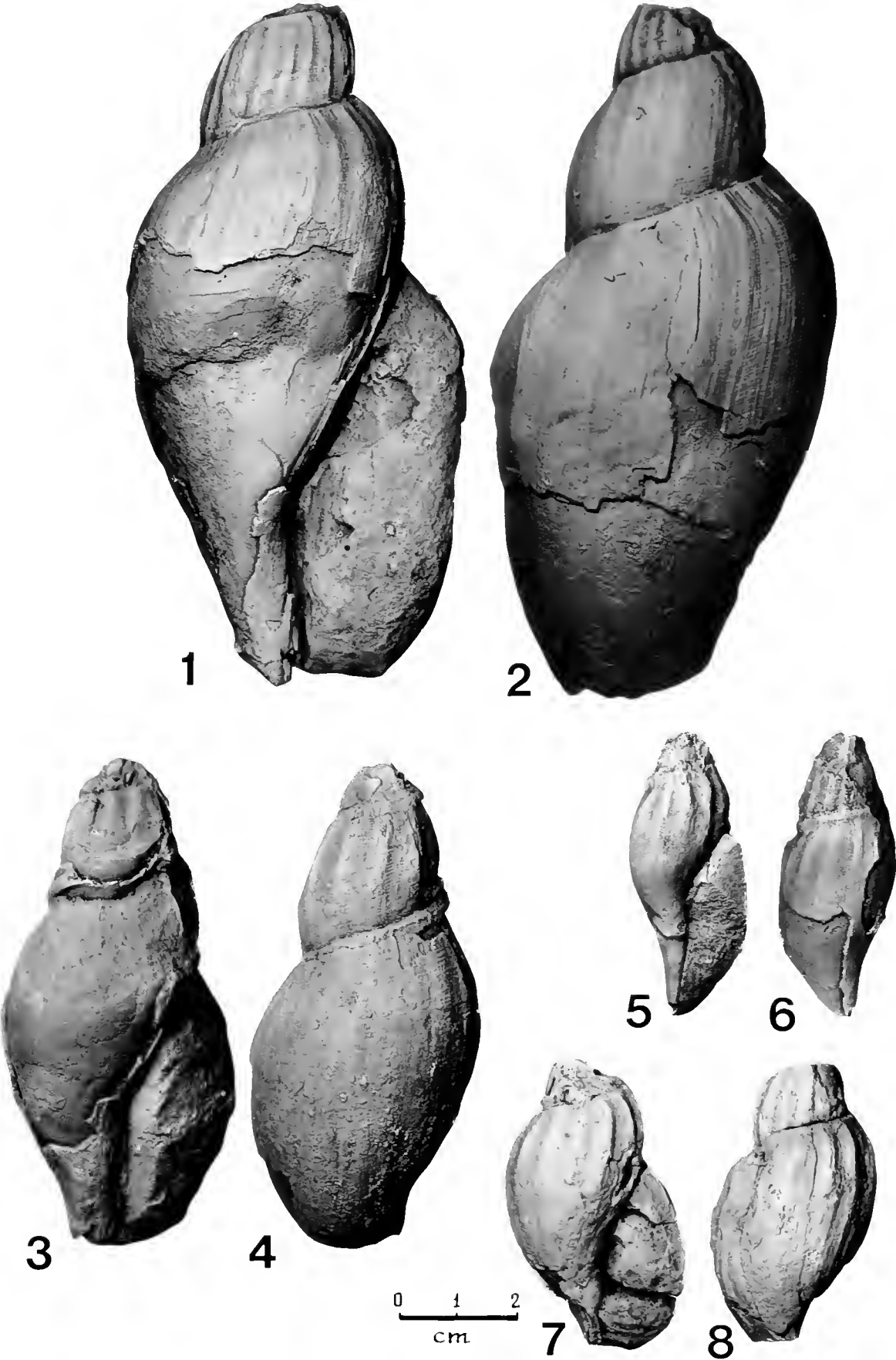
Stratigraphic range: Known only from the Upper part of the Alugian Formation of eastern Kamchatka. Oligocene.

Comparative remarks: Although similar to *Fulgoraria shutoi* Shikama, 1967, from the Kishima Formation (Oligocene, Japan), this new species differs in having a more elongated last whorl, narrower axial folds, nearly smooth body whorl, and only a single fold rather than several strong ones.

Fulgoraria (Musashia) olutorskiensis (L. Krishtofovich, 1973)
Figures 11, 12, 15, 16

Miolepleiona oregonensis Khomenko, 1933:25, pl. 6, fig. 20
Miolepleiona olutorskiensis L. Krishtofovich, 1973:77, pl. 22, figs. 5, 9.
Musashia olutorskiensis Devyatilova & Volobueva, 1981:128, pl. 32, fig. 2

Figures 1, 2. *Fulgoraria (Musashia) novoilpinica*, new species. Holotype, USNM 468649, 119.5 mm, Alugian Formation, Oligocene. Figures 3, 4. *Fulgoraria (Musashia) genuata*, new species. Holotype, USNM 468650, 84.5 mm, Alugian Formation, Oligocene. Figures 5, 6. *Fulgoraria (Neopsephaea) tenuis* (Shikama, 1967). GI 1164, 49.2 mm, Matchigarian Formation, Oligocene. Figures 7, 8. *Fulgoraria (Musashia) tiltschukensis*, new species. Holotype, USNM 468652, 51.1 mm, Alugian Formation, Oligocene.



Musashia (Musashia) sp. Gladenkov, Sinelnikova & Bratseva, 1987:57, pl. 15, fig. 2.

Description: Shell oblong, fusiform, relatively thin, with 5–6 postnuclear whorls. Body whorl comprises approximately $\frac{2}{3}$ of shell height. Suture slightly depressed, with narrow subsutural band. Aperture elliptical, acute posteriorly. Inner lip arched, with one narrow columellar fold. Callus thin, narrow. Shell surface nearly smooth, with thin growth striae and very fine, raised spiral threads.

Material examined: Holotype—CMG 21/10285, length 130.4 mm, width 48 mm, Pachatchi River, Olutorsky Region, eastern Kamchatka, Russia, “Ilpinian” Formation, Oligocene; Paratype—19/10285, Gulf of Olutorsk, Govenia Peninsula, eastern Kamchatka, Russia, Oligocene; GI 1486, GI 4055—both from Ilpinsky Peninsula, northeastern Kamchatka, Russia, Alugian Formation, Oligocene; 9 incomplete shells and fragments and 7 molds.

Type locality: Olutorsky Region, northeastern Kamchatka, Russia.

Stratigraphic range: Known from the Oligocene formations of northeastern Kamchatka; abundant in the Alugian Formation of the Ilpinsky Peninsula.

Comparative remarks: With its nearly smooth sculpture, this species most closely resembles *Fulgoraria (Musashia) nagaoi* (Shikama, 1967) from the Poronai Formation (Eocene–Oligocene of Hokkaido), but differs in being more elongated, in having fine spiral sculpture, and in having a distinct subsutural band.

Fulgoraria (Musashia) genuata new species
Figures 3, 4, 19

Description: Shell oblong, fusiform, slender, with three stout, preserved whorls, and estimated 5–6 postnuclear whorls in intact specimens. Body whorl comprises $< \frac{1}{2}$ total shell length. Suture shallow, slightly impressed. Aperture elliptical. Columella with one weak columellar fold. Sculpture of straight, smooth, widely spaced axial ribs (4 per whorl), most prominent on early whorls. Spiral sculpture of numerous, fine, slightly raised threads covering shell surface.

Material examined: Holotype—USNM 468650, length 84.5 mm, width 40.0 mm; Paratype—GI 40721, length 75.9 mm, width 46.1 mm; both from type locality.

Type locality: Northwestern part of Ilpinsky Peninsula, northeastern Kamchatka, Russia. Alugian Formation. Oligocene.

Stratigraphic range: Known only from the Alugian Formation of the Ilpinsky Peninsula. Oligocene.

Comparative remarks: Although similar to *Fulgoraria (Musashia) fujimotoi* (Kanno, 1958) from the Hikokubo Formation (Oligocene–Miocene, Japan), this new species differs in having stouter whorls and a lower spire, in having one instead of two columellar folds, and in having finer spiral sculpture.

Fulgoraria (Musashia) cordata new species
Figures 13, 14

Description: Shell elongate, fusiform, slender, with four postnuclear whorls, short siphonal canal and narrowly channeled suture. Body whorl comprises approximately $\frac{1}{4}$ of shell length. Aperture oblong, with narrow posterior angle. Columella with one weak columellar fold. Axial sculpture of low, rounded ribs (≈ 12 per whorl on penultimate whorl). Axial ribs crossed by fine, closely spaced spiral lines.

Material examined: Holotype—USNM 468651, length 59.1 mm, width 24.3 mm; Paratype 1—GI 4063/2, length 50.5 mm, width 26.5 mm; Paratype 2—GI 40531, length 62.8 mm, width 26.5 mm; two molds, three fragments and one impression; all from the type locality.

Type locality: Northwestern part of Ilpinsky Peninsula, northeastern Kamchatka, Russia. Upper part of the Alugian Formation. Oligocene.

Stratigraphic range: Known only from the type locality.

Comparative remarks: This new species is most similar to *Fulgoraria (Musashia) weaveri* (Tegland, 1933) of the Blakeley Formation (Oligocene, Washington, USA), but has a more elongated shell, more numerous axial ribs, and much stronger spiral threads.

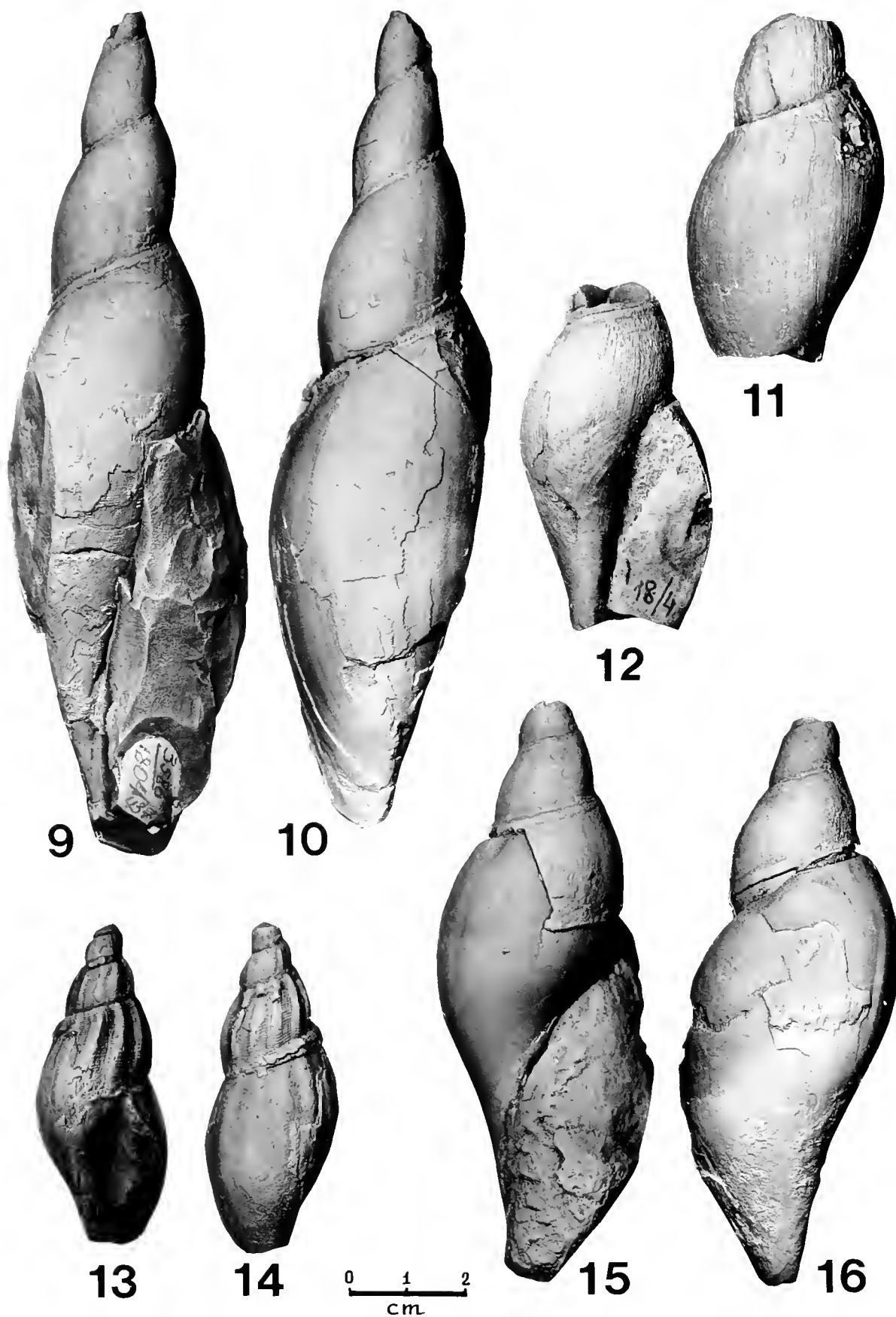
Fulgoraria (Musashia) tiltschikensis new species
Figures 7, 8, 18

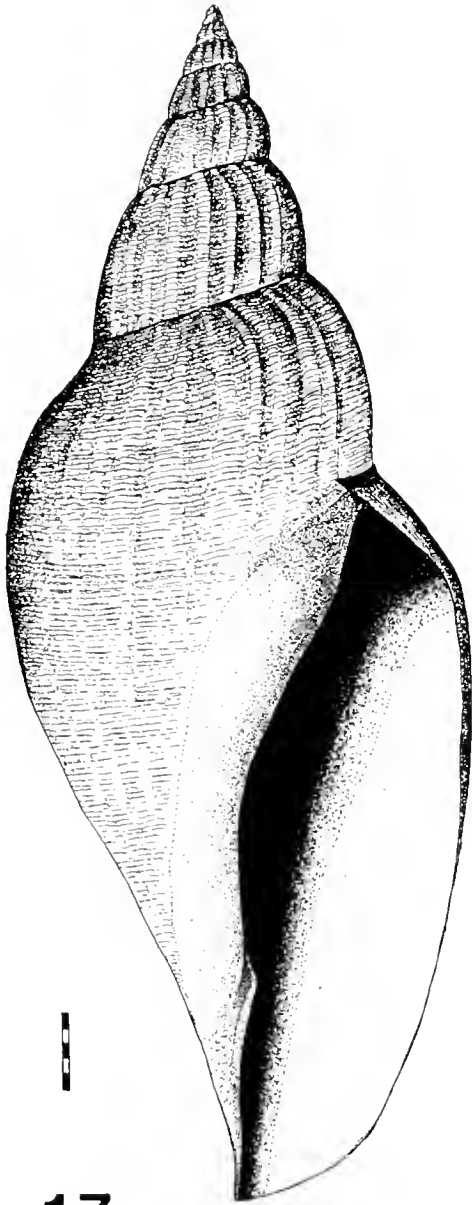
Description: Shell globosely fusiform, solid. Teleoconch of about 5 whorls. Suture narrowly pressed. Body whorl comprises $\frac{2}{3}$ shell length. Aperture semioval, with thin, narrow callus. Inner lip with one weak, subvertical columellar fold. Axial sculpture of rounded arcuate ribs (13 on body whorl). Spiral sculpture lacking.

Material examined: Holotype—USNM 468652, length (incomplete) 51.1 mm, width 29.5 mm, from the type locality; Paratype GI 40724, length (incomplete) 65.0 mm, width 37.6 mm, Ilpinsky Peninsula, northeastern Kamchatka, Russia. Alugian Formation, Oligocene.

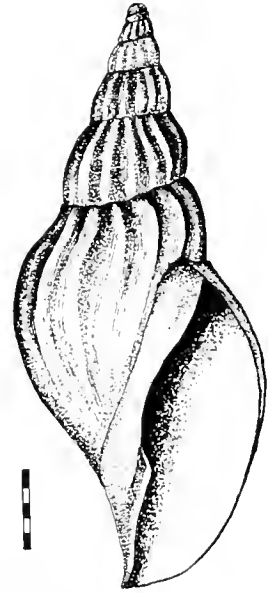
Type locality: Korf Settlement, Coal River, northeastern Kamchatka, Russia. Alugian Formation. Oligocene.

Figures 9, 10. *Fulgoraria (Nipponomelon) cf. tokunagai* (Kanehara, 1937). GI 3586/1804, 149 mm, “*Laternal*” Sandstones, Karaginsky Island, Oligocene–Lower Miocene (?). **Figures 11, 12, 15, 16.** *Fulgoraria (Musashia) olutorskensis* (L. Krishtovich, 1973). **11, 12.** GI 1486, 61.8 mm. **15, 16.** GI 4055, 103.9 mm, Alugian Formation, Oligocene. **Figures 13, 14.** *Fulgoraria (Musashia) cordata*, new species. Holotype, USNM 468651, 59.1 mm, Alugian Formation, Oligocene.

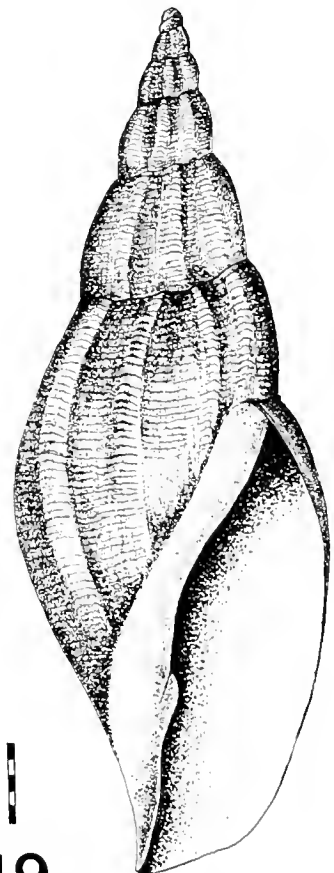




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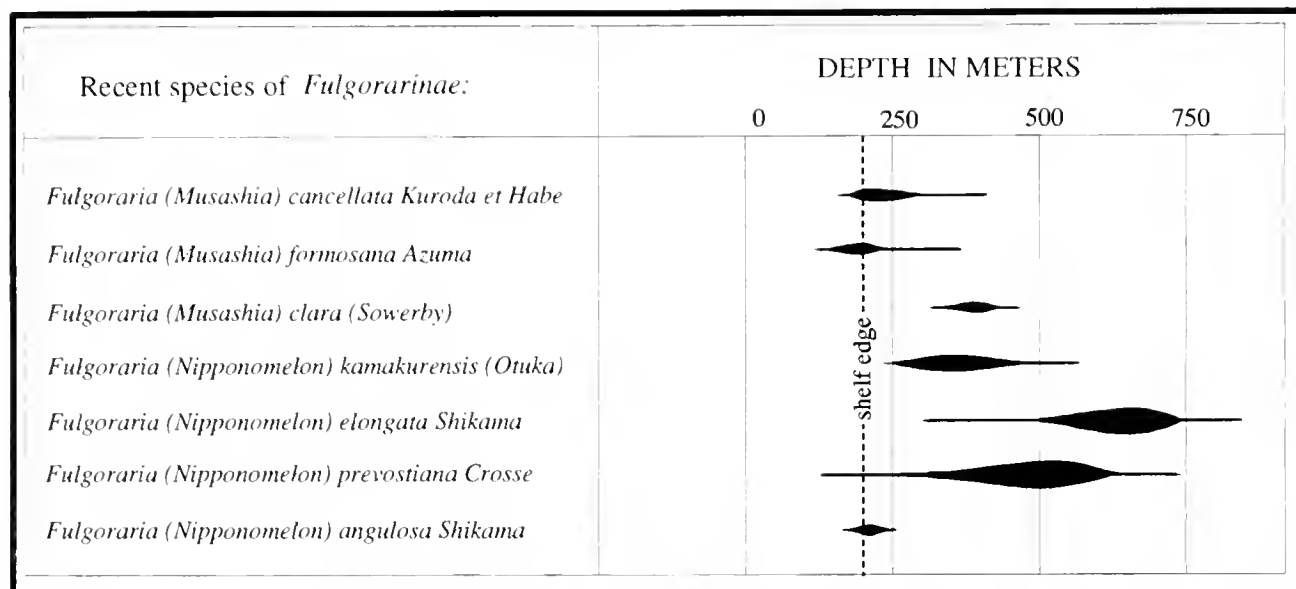


Figure 20. Bathymetric distributions of Recent species of Fulgorariinae of Japan and adjacent seas, based on data in Shikama (1967), and Weaver and du Pont (1970). Thickness of lines indicates relative abundance.

Stratigraphic range: Known only from the Alugian Formation of northeastern Kamchatka, Russia. Oligocene.

Comparative remarks: This species resembles *Fulgoraria (Musashia) shikamai* Moore, 1984, from the Poul Creek Formation (Alaska, USA) and the Clallam and Twin River Formations (Washington, USA), but this new species has more sharpened axial ribs and finer spiral threads.

Subgenus *Nipponomelon* Shikama, 1967

Fulgoraria (Nipponomelon) cf. *tokunagai* (Kanehara, 1937)

Figures 9, 10

Psephaea tokunagai Kanehara, 1937:16–18, pl.2, figs. 2–5

Fulgoraria (Psephaea) prevostiana Crosse, Shikama, 1954 pl 6, fig. 26.

Fulgoraria tokunagai Kamada, 1962:192, pl.21, figs. 5–8.

Musashia (Nipponomelon) tokunagai Shikama, 1967 100–101, pl.14, fig. 4.

Musashia tokunagai Devyatilova & Volobueva, 1981:128, pl.33, fig. 1.

Original Description: "Shell tall and high spired, apical angle about 25 degrees. Suture slightly impressed with narrow shelf around it. Surface ornamented with axial folds, which may be somewhat accentuated above and tend to disappear on the body whorl. Spirally grooved regularly, also over the folds. Aperture spindle shaped, obliquely notched posteriorly, with narrower anterior canal. Inner lip provided with two columellar folds and

covered by a thin callus, which adheres to the columella and thickens anteriorly."

Material examined: One specimen, GI 3586/1804, length 149 mm, width 62.2 mm, from the "Laternula" sandstones, Karaginsky Island, Gnunvayam River, Russia. Oligocene-Lower Miocene (?).

Type locality: Yanagaya bed, Nagakura coal mine, Yumoto, Iwaki City, Fukushima Prefecture, Honshu, Japan. Lower Miocene.

Stratigraphic range: "Laternula" sandstones, Karaginsky Island, Gnunvayam River, Russia, Oligocene-Lower Miocene (?), to Yanagaya bed, Nagakura coal mine, Yumoto, Iwaki City, Fukushima Prefecture, Honshu, Japan. Lower Miocene.

Comparative remarks: *Fulgoraria tokunagai* is characterized by a large size, high spire, large protoconch, and numerous axial folds. The spiral sculpture on the single specimen from Karaginsky Island is poorly preserved, but this specimen retains visible traces of the axial folds and thin spiral grooves. The shape and size of this specimen, especially the features of the aperture, suture, and sculpture, are the same as in typical *F. tokunagai*. However, the Russian specimen differs from the type in having a single columellar fold rather than two. This difference, together with the poor preservation of this shell puts the species determination of this specimen in some doubt.

Figure 17. *Fulgoraria (Musashia) novoilpinica*, new species. Reconstructed drawing of holotype. **Figure 18.** *Fulgoraria (Musashia) tilitschikensis*, new species. Reconstructed drawing of holotype. **Figure 19.** *Fulgoraria (Musashia) genuata*, new species. Reconstructed drawing of holotype. Scale bars = 10 mm.

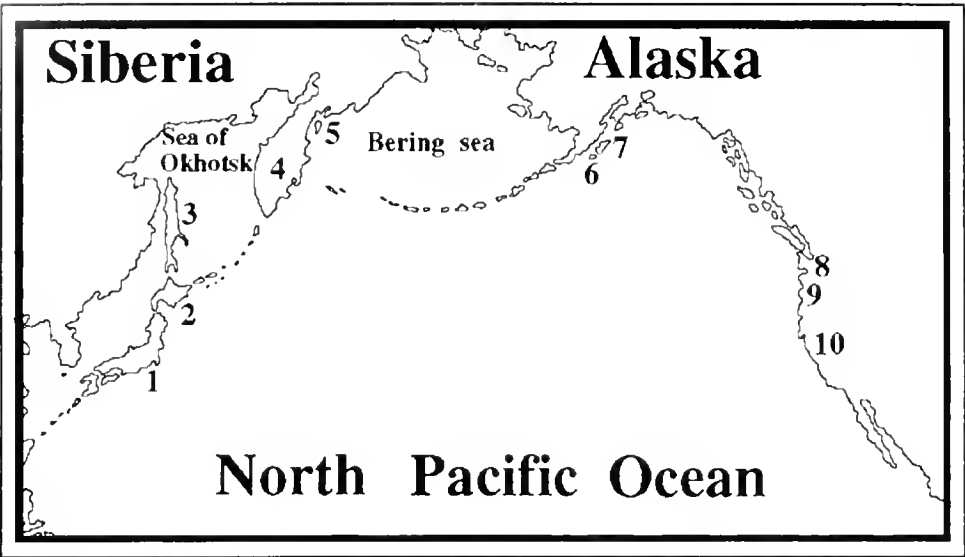


Figure 21. Fossil localities of Oligocene Fulgorarinae in the North Pacific referred to in the text. 1—Honshu Island, 2—Hokkaido Island, 3—Sakhalin Island, 4—Kamchatka Peninsula, 5—Karaginsky Island, 6—Sitkinak Island, 7—Kodiak Island, 8—Oregon, 9—Washington, 10—California.

Subgenus *Neopsephaea* Takeda, 1953

Fulgoraria (*Neopsephaea*) *tenuis* Shikama, 1967
Figures 5,6

Musashia (*Neopsephaea*) *tenuis* Shikama, 1967:116–117, pl.13, figs. 3,4

Original description: “Shell small in size, slender, fusiform and with low spire. Suture shallow and there is no subsutural band. Last whorl vaulted at middle and aperture relatively narrow. Surface of whorl smooth and axial ribs relatively few and weak, about 11 in penulti-

mate whorl, gradually becoming obsolete anteriorly. Tip of columella straight and narrow. There may be one columellar plait”.

Supplemental description: Shell is rather slender, elongate, fusiform, with about 5 (when restored) whorls separated by a shallowly impressed suture. Body whorl and aperture comprising slightly more than $\frac{2}{3}$ of total shell length. Aperture elliptical, forming acute angles at anterior and posterior margins. Siphonal notch relatively narrow. Outer lip thin, simple. Columella with one weak columellar fold. Callus very thin. Shell surface smooth,

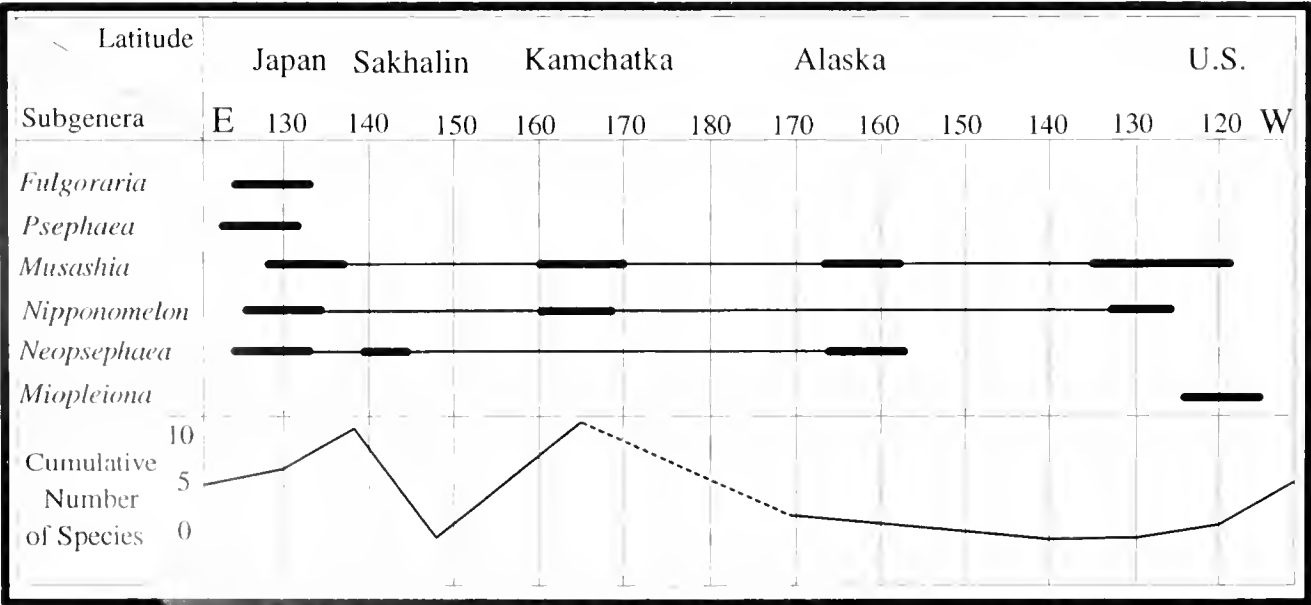


Figure 22. Geographic distribution of the subgenera of *Fulgoraria*, and their species diversity during the Oligocene.

with thin growth lines. Axial sculpture of low, rounded ribs (11–12 on body whorl) that disappear on anterior portion of body whorl.

Material examined: One specimen, GI 1164, length 49.2 mm, width 22 mm, near Lake Matschigar, central Sakhalin Island, Russia, Matschigarian Formation, Oligocene.

Type locality: Zochuku Sandstone, Kishima Group, Nagasaki Prefecture, Kyushu, Japan. Oligocene.

Stratigraphic range: Near Lake Matschigar, central Sakhalin Island, Russia, Matschigarian Formation, Oligocene, to Zochuku Sandstone, Kishima Group, Nagasaki Prefecture, Kyushu, Japan, Oligocene.

Comparative remarks: This species is closely allied to *Fulgoraria* (*Neopsephaea*) *antiquior* Takeda, but may be distinguished by its more swollen body whorl, narrower aperture with distinctive posterior margin, smooth surface, and axial ribs that are fewer in number or entirely obsolete.

DISCUSSION

The lithology of the Alugian Formation of the Ilpinsky Peninsula in eastern Kamchatka consists of gray to dark gray claystones and clays. This formation has a total thickness of about 950 meters, and is continuous, lacking hiatuses or internal unconformities. No shallowing or deepening trends are evident within the section. The strata contain numerous carbonate concretions ranging in size from 1 cm to several meters. Some of the claystone beds are delicately laminated. These types of sediments are indicative of soft bottom environments.

Molluscan remains are quite common, but are not concentrated in particular layers or lenses. Fossils occur sporadically throughout the section, both in concretions and within the matrix. The molluscan fauna does not exhibit many changes from the bottom to the top of the formation. These data point to a depositional regime comprising relatively rapid and uninterrupted sedimentation (Kidwell, 1985).

Species diversity in the molluscan assemblage of the Alugian Formation is low. The most abundant taxa occurring together with fulgorariine volutes include *Trominina bicordata* (Hatai & Koike, 1957), *Trominina ishikariensis* (Hayasaka & Matsui, 1951), *Neptunea ezoana* Takeda, 1953, *Bathybembix sakhalinensis korjakensis* Volobueva, 1981, *Optoturris* (?) sp., *Turritella* sp., *Cryptonatica* spp., *Acila praedivaticata* Nagao & Huzioka, 1941, and *Cyclocardia ilpinensis* Pronina, 1973. All these taxa have relatively broad bathymetric ranges, occurring from lower neritic to bathyal depths (Hall, 1960; Noda, 1975; Scarlato, 1981; Moore, 1984).

Recent species of Fulgorariinae are mainly bathyal animals, dredged most often from depths of 250 to 700 or more meters (fig. 20). Bathymetrically, the bathyal zone extends from a mean depth of 200 m to 2000 m, and thermally, from the 15°C isotherm in low latitudes

down to the –3°C isotherm in high latitudes. Substrates are predominantly fine silts, muds, and oozes (Encyclopedia of Oceanography, 1974; Hickman, 1974). Oxygen isotope analyses of five *Cyclocardia ilpinensis* shells collected from the bottom through the top of the Alugian Formation allowed the estimation of paleotemperatures as ranging from 3°C to 5°C. These data indicate that water temperatures remained quite uniform during the deposition of this formation, and support the hypothesis of a bathyal environment. When compared to Recent bathyal bottom temperatures, these data suggest that the climatic conditions during Alugian deposition were similar to those found between 32°N and 45°N, and approximate the temperatures that define the distribution of Recent species of *Fulgoraria*. Paleotemperatures estimated for the Alugian Formation exhibit some correlations with those estimated for Oligocene formations of the western coast of North America. Paleotemperatures of the Blakeley Formation (*Echinophoria apta* zone), which contains five species of Fulgorariinae, were estimated as to be 5–8°C. The remains of *Aturia* nautiloids in great abundance, which may have required a temperature of at least 16°C could be explained by post-mortem transport of empty shells, which is fairly common with Recent *Nautilus*. Paleodepth was thought to range from 100 m to 350 m (Moore, 1984). Similarly, the Narrow Cape Formation of Sitkinak Island (Alaska), which contains three species of Fulgorariinae, was deposited in the outer neritic zone of the continental shelf (Allison, 1978). A comparison of the Narrow Cape data with that of Recent Alaskan mollusks suggests a paleodepth of 100–200 m, and water temperatures of 10–12°C in summer months during the Oligocene (Allison & Marinovich, 1981). According to Hall (1964), this type of marine climate can be defined as cool-temperate. The Recent species *Fulgoraria* (*Nipponomelon*) *prevostiana* (Crosse, 1878) has been dredged from depths of 110–732 m off western Hokkaido, Japan, at a bottom temperature of 11.8°C (Weaver & du Pont, 1970:45). Water temperatures for the Alugian Formation thus seem to be colder than those in western America. These data more probably suggest a deeper depositional environment for the Alugian Formation, perhaps no shallower than 400–500 m, and therefore colder water.

Oligocene climatic conditions, therefore, must have been quite favorable for a wider distribution of fulgorariine volutes that is seen today. This is clearly supported by the fossil record (fig. 21). Based on the stratigraphic distribution and analysis of total species diversity of Cenozoic volutes, it has been deduced that the Oligocene–Early Miocene was the first period of wide distribution and high species diversity of northern Pacific Fulgorariinae (Oleinik, 1990). There was, however, an appreciable amount of endemism, especially at the subgeneric level. *Fulgoraria* s.s. and *Psephaea*, for example, were restricted to the western Pacific, while *Miopsephaea* is known only from the northeastern Pacific. These restricted geographic ranges may have been caused by different centers of origin of the North Pacific Fulgo-

rariinae, or were the results of differing dispersal strategies. Other subgenera, such as *Musashia* and *Nipponomelon*, were abundant throughout the north Pacific. Total species diversity of Fulgorariinae, however, did not vary appreciably during the Oligocene of the north Pacific (fig. 22).

ACKNOWLEDGMENTS

I thank Dr. Yuri B. Gladenkov and Dr. Valentina N. Sinelnikova, of the laboratory of Phanerozoic Stratigraphy of the Geological Institute of the Russian Academy of Sciences, for providing material; Dr. Sergei I. Kiyashko, of the Institute of Marine Biology in Vladivostok for the oxygen isotope analyses. Photographs of the shells were taken by Mr. Andrew A. Okunev of the Geological Institute, Moscow. My special thanks to Dr. M. G. Harsenewych, National Museum of Natural History, Smithsonian Institution, Washington, D.C., Dr. E. J. Petuch, Florida Atlantic University, Boca Raton, Florida, and Dr. L. K. Marinovich, U.S.G.S., Menlo Park, California for critical review of the manuscript.

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A New Species of Columbelloid Gastropod from the Old World Tropics

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ABSTRACT

Cotonopsis monfilsii new species, is described from off Senegal, West Africa in 230–500 m. The generic assignment is made on the basis of shell, opercular, and radular characters. The radula is typically columbellid, whereas the shell morphology lacks some characteristics of the “*Strombina*” gastropods. Therefore, the placement in the *Strombina*-group genus *Cotonopsis* is tentative. *Metula dockeryi* new name is proposed to replace *Metula inflata* Dockery, 1984, not *Metula inflata* (Houbrick, 1984).

Key Words: Prosobranchia, Columbelloidae, *Cotonopsis*, Buccinidae, *Metula*, west Africa, new species, new name.

INTRODUCTION

During the past five years, we have received from several shell dealers specimens of an apparently new species of columbellid gastropod for study and report. The taxonomic placement of these shells could not be made with certainty until the morphology of the radula was determined. A radula was eventually found and proved to be typically columbellid in form. As a result, this gastropod can be assigned provisionally to the *Strombina*-group genus *Cotonopsis*.

I take pleasure in describing this new species in honor of Paul Monfils, who was the first to call this perplexing species to my attention.

A review of the literature disclosed that a replacement name was required for a fossil species of *Metula*. A new name is provided for *Metula inflata* Dockery, 1984, not *Metula inflata* Houbrick, 1984.

ABBREVIATIONS

AMNH = American Museum of Natural History, New York

LACM = Los Angeles County Museum of Natural History, California.

SYSTEMATICS

Superfamily: Buccinoidea Rafinesque, 1815

Family: Columbelloidae Swainson, 1840

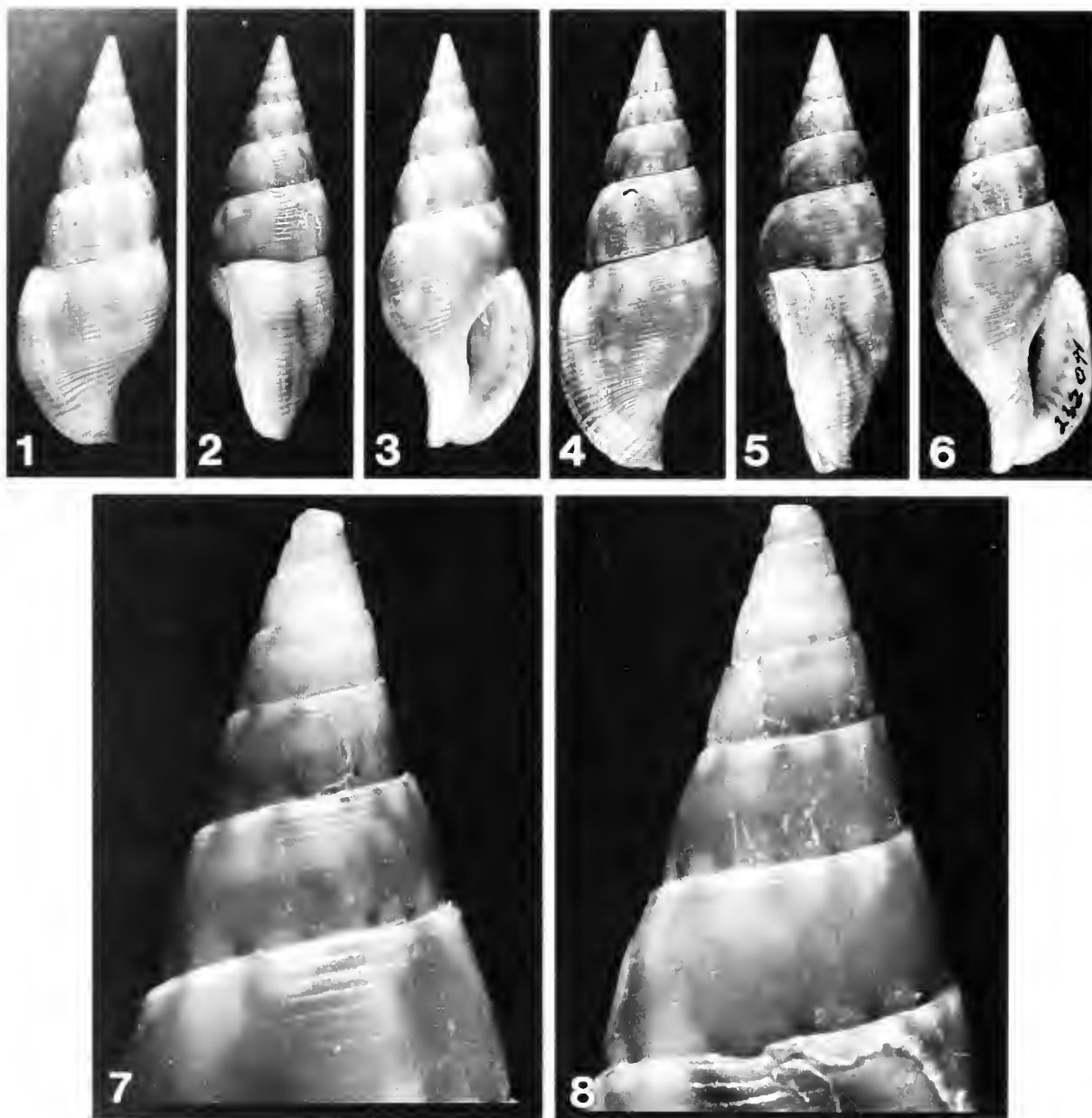
Genus *Cotonopsis* Olsson, 1942

Type species (by original designation): *Strombina (Cotonopsis) panacostariceus* Olsson, 1942, Pliocene of the Burica Peninsula, Costa Rica, Charco Azul Formation

Cotonopsis monfilsii new species
(figures 1–10)

Description: Shell solid, fusiform, whorls inflated without a sutural ramp; protoconch of 3½ smooth, convex whorls; teleoconch of 7½ convex whorls, sculptured with numerous fine spiral lirae, numbering about 18 on the penultimate whorl and about 32 on the body whorl. Some spiral lines bifid; lirae not consistently evenly spaced. Thickened varix formed on body whorl above the rim of the aperture. Aperture ovate, inner lip terminally thin, but with a sublabial ridge with 10 lirate teeth; columella with 4–5 weak folds; siphonal canal open, short, narrow. Fasciole indistinct. Periostracum brownish tan. Background color brownish buff-tan with broken whitish bands below the suture and with axial blotches interrupting the tanish coloration. Aperture white. Operculum thin, corneous, lenticular with a terminal nucleus at edge. Radular ribbon (figs. 9, 10) rachiglossate, typically columbellid (cf. Radwin, 1977, fig. 22b). Rachidian tooth a narrow, nearly rectangular plate. Lateral tooth shaft-like with barbed base, tip of shaft with two hooked cusps.

Material examined: Holotype (AMNH 232519) and 3 paratypes (AMNH 232091) from the type locality; 5 Paratypes (AMNH 232092) dredged in 300–350 m, on muddy bottom, off St. Louis, Senegal, November, 1987, ex-Northeast Natural History Imports; 3 Paratypes (AMNH 232152) dredged in 450–500 m, on muddy-sand bottom, off St. Louis, Senegal, ex-Northeast Natural History Imports; 6 referred specimens (5 specimens, AMNH



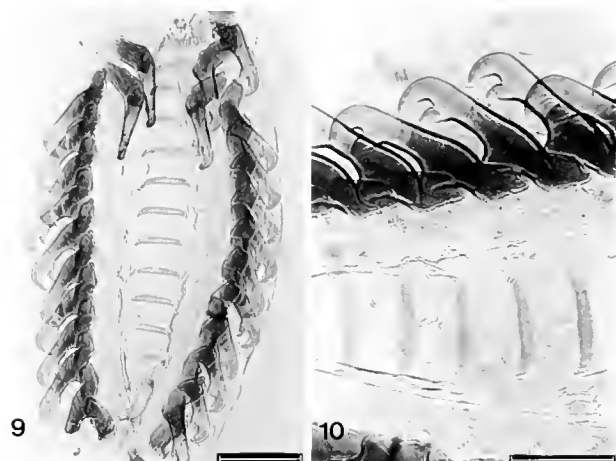
Figures 1-8. *Cotonopsis monfilsii* n. sp. 1-3, holotype (AMNH 232519). 4-6, paratype (AMNH 232091); figs. 1-6 $\times 1.5$. Figs. 7, 8, paratype (AMNH 232092), spire enlarged to show detail of early whorls; figs. 7, 8, $5.0\times$

232176; 1 specimen, LACM 146956) dredged on silty-sand bottom, 230-260 m, off Casamance Province, Senegal ($12^{\circ}50'N, 15^{\circ}0'W$), ex-Northeast Natural History Imports; 2 referred specimens (AMNH 255056) trawled in deep water from off the Dakar harbor entrance, Senegal ($14^{\circ}40'N, 17^{\circ}26'W$), ex-Mal de Mer Enterprises. See Table 1 for shell measurements.

Type locality: dredged in 300 m off St Louis, Senegal, West Africa, ($16^{\circ}02'N, 16^{\circ}30'W$) by Marcel Pin, 1987, ex-Abbey Specimen Shells.

Distribution: Known only from off Senegal, West Africa in 230 to 500 meters.

Remarks: The shells of the present specimens resemble certain "*Strombina*"-group gastropods (such as *Cotonopsis*), but they are also in some respects reminiscent of certain buccinid gastropods (eg. *Pisania*, *Metula*, etc.). Before the nature of the radula was known, I asked several colleagues for their opinions based on the examination of photographs or the study of the specimens. Some of them referred the specimens to the buccinid genus *Pisania* Bivona-Bernardi, 1832, in the subfamily Pisaniinae Gray, 1857:13, formerly credited to Tryon, 1881:98 (see Cernohorsky, 1971:138; 1975:192; Beu and Maxwell, 1987:56; and Bouchet, 1988:149, for comments on the subfamilial status of Pisaniinae in Buccinidae, and



Figures 9, 10. *Cotonopsis monfilsii* n. sp. 9, holotype (AMNH 232519), radula, about one-third of the ribbon. 10, detail of the rachidian teeth, fig. 9, scale bar = 100 μ m, fig. 10, scale bar = 200 μ m, courtesy of J. H. McLean

its rejection without an explanation at the subfamilial level by Ponder and Warén, 1988:305). The resemblance of the new species to Recent species of *Charitodoron* (Mitridae) from South Africa was also suggested (see Lozouet, 1991:206, figs. 26–30). Other colleagues believed the Senegalese specimens to be an undescribed columbellid species referable to *Cotonopsis* (*sensu stricto*).

With the recovery of a radula from a dried body of the new species, the placement of the new species in the family Columbellidae can be confirmed. The radular characters are typically columbellid in form (figs. 9, 10). As in *Cotonopsis argentea* (Houbrick, 1983:352, fig. 2), the radular dentition consists of rachidian teeth that are thin, narrow and form a rectangular plate. A wide space separates the rachidian teeth from the lateral teeth, which are composed of a shaft with an enlarged base and are tipped with two hooked cusps. The shells of the new species possess the thickened varices of *Strombina*-group gastropods, but the apertural dentition of the inner lip differs in having evenly spaced lirate denticles of equal size. These are comparable to those of the buccinid genus *Bartschia* Rehder (1943:199, pl. 20, fig. 17; Olsson and Bayer, 1972:924, fig. 14). Furthermore, *Bartschia significans*, the type species, has strongly cancellate sculpture, whereas the new species possesses fine spiral lirae. The radular characters of *Bartschia* are unknown, but on shell features, Beu and Maxwell (1987:62) believe *Bartschia*, together with *Metula* H. and A. Adams (1853: 84; Emerson, 1986:27), to be closely related to the buccinid genus *Colubraria* Schumacher, 1817. Some of the western Atlantic species of *Metula* [e.g. the West Indian *M. (Agassitula) agassizi* Clench and Aguayo, 1941:179, pl. 14, fig. 4; Olsson and Bayer, 1972:917, fig. 11 and the east African *M. (Kanamaria) rehderi* (Kilburn, 1977: 193, fig. 21)] superficially resemble the new species. Bouchet (1988:150, fig. 1) illustrated the typically buc-

Table 1. Shell dimensions and proportions of the specimens of *Cotonopsis monfilsii* n. sp. n = 20 specimens. Width includes terminal varix on body whorl. Measurements in mm

Type specimens	Height	Width	Width-height
*AMNH 232519 (holotype)	40.1	14.9	0.37
AMNH 232091 (paratype 1)	41.7	15.2	0.36
AMNH 232091 (paratype 2)	37.2	13.7	0.37
AMNH 232091 (paratype 3)	37.1	13.6	0.37
AMNH 232092 (paratype 1)	41.1	14.4	0.35
AMNH 232092 (paratype 2)	37.9	13.4	0.35
AMNH 232092 (paratype 3)	37.1	13.8	0.35
AMNH 232092 (paratype 4)	37.5	13.6	0.36
AMNH 232092 (paratype 5)	36.2	12.8	0.35
AMNH 232152 (paratype 1)	40.4	14.6	0.36
AMNH 232152 (paratype 2)	36.9	12.8	0.35
AMNH 232152 (paratype 3)	34.5	12.6	0.37
Referred specimens			
AMNH 232176, a	39.7	14.5	0.37
AMNH 232176, b	36.3	13.8	0.38
AMNH 232176, c	36.1	13.9	0.39
AMNH 232176, d	35.0	14.0	0.40
AMNH 232176, e	34.9	13.7	0.40
LACM 146956	36.2	13.9	0.38
AMNH 255056, a	39.1	14.1	0.36
AMNH 255056, b	38.6	13.4	0.35
Mean	37.1	13.8	0.36
Range	34.5–	12.6–	0.35–
	41.7	15.2	0.40

* Radula extracted.

cinid radula of his new species, *Metula africana*, and concluded the radular morphology is significantly different from that of the buccinid genus *Pisania*.

The placement of the new species in the genus *Cotonopsis* based on shell characters is tentative. As the genus is defined by Jung (1989:158), the teleoconch whorls are smooth or axially sculptured. In the new species, the teleoconch sculpture is composed of fine spiral lines and no axial sculpture is present. *Cotonopsis* is represented in the tropical western Atlantic by one species (*C. argentea*). The remainder of the 15 species of *Cotonopsis* recognized by Jung (1989), 2 fossil and 12 living species, occur in the west American tropical zone. Previously, the *Strombina*-group gastropods were believed to be restricted to the New World tropics, dating from the Miocene to the present, with only 3 of the 35 living species occurring in the western Atlantic (Jung, 1989:4). Therefore, the presence of a species of *Cotonopsis* in west African waters may reflect a separate lineage of these columbellids that may eventually be determined to require recognition as a new genus-group taxon.

REPLACEMENT NAME FOR A HOMONYM

During my review of the literature for this paper, I noted a homonymic species-group name in *Metula* (Buccinidae). *Metula (Metula) inflata* Dockery in MacNeil and

Dockery (1954:331, pl. 52, fig. 3; published in "November, 1984", *teste* D. T. Dockery III, in *litt.*, Dec. 9, 1991) is a junior secondary homonym of *Acamptochetus* [= *Metula*] *inflatus* Houbriek (1984:421, fig. 1; published July 6, 1984). I here rename *Metula inflata* Dockery, 1984 (not *Metula inflata* [Houbriek, 1984]), as *Metula dockeryi* Emerson, NEW NAME. Dockery's taxon is a Paleogene fossil from Mississippi and Houbriek's taxon is a Recent Philippine species.

Acamptochetus Cossmann (1901:123; type species by original designation: *Murex mitraeformis* Brocchi, 1814) is a junior subjective synonym of *Metula* H. and A. Adams (1853:84; type species by subsequent designation Kobelt, 1876: *Buccinum clathratum* Adams and Reeve, 1850, [not Kiener, 1834, nor Anton, 1839] = *Metula amosi* Vanatta, 1913:22), as noted by Emerson (1986:27) and Beu and Maxwell (1987:62) and accepted by Bouchet (1988:149).

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The Association between the Gastropod *Buccinanops cochlidium* (Dillwyn, 1817) and the Sea Anemone *Phlyctenanthus australis* Carlgren, 1949 in Patagonian Shallow Waters

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ABSTRACT

The association between *Buccinanops cochlidium* (Dillwyn) and *Phlyctenanthus australis* Carlgren is described. Both species inhabit in the sandy infralittoral of Puerto Pirámide, Chubut Province, Argentina. The densities and percentages of gastropods with anemones attached are reported, and the possible benefits to the sea anemone and the gastropod are discussed.

Key words: Symbiosis, Ecology, Anemones, *Buccinanops*.

INTRODUCTION

The association between actinians and gastropod shells occupied by hermit crabs has been frequently described (e. g. Faurot, 1910, 1932; Brunelli, 1913; Ross, 1960; Ross & Sutton, 1961a, 1961b; McLean and Mariscal, 1973; Balasch *et al.*, 1977; Brooks and Mariscal, 1986). However few papers have been published describing the relationship between actinians and living gastropods in the South Atlantic (Bellisio *et al.* 1972; Arnaud, 1978).

This paper reports on the association between *Buccinanops cochlidium* (Dillwyn, 1817) and *Phlyctenanthus australis* Carlgren, 1949, from northern Patagonia.

MATERIALS AND METHODS

Specimens of *Buccinanops cochlidium* and *B. globulosum* were collected during November 1989 and October 1990 while SCUBA diving at depths of 5-11 m in the sandy infralittoral zone off Puerto Pirámide (42°35'S, 64°17'W), Chubut Province, Argentina. In February 1992, 18 samples were collected from various depths. The information obtained from each sample included depth, area, number of individuals of each species of gastropod, and number of anemones attached per gastropod. Data from samples were combined to give a general pattern for Puerto Pirámide. Depth was determined using a capillary depth gauge (Dacor model LCG & MCG).

The material was first relaxed at low temperatures and

then preserved in 70 % formalin. The specimens are housed at the División Zoología Invertebrados, Museo de Ciencias Naturales, La Plata, Buenos Aires, Argentina.

RESULTS

The anemone *Phlyctenanthus australis* commonly covers the entire dorsal surface of the mollusk shell with its pedal disc, leaving only the aperture free (fig. 4). In some cases as many as two specimens of *P. australis* were attached to a single gastropod (fig. 5). Usually only a single anemone is attached either to the spire or the body whorl. When *in situ* specimens are viewed from above, only the completely extended oral disc of the anemone is visible, with the tip of the siphon of *B. cochlidium* extending from beneath its edge. The gastropods usually remain completely buried. Occasionally, crawling specimens with more than one attached anemone were observed.

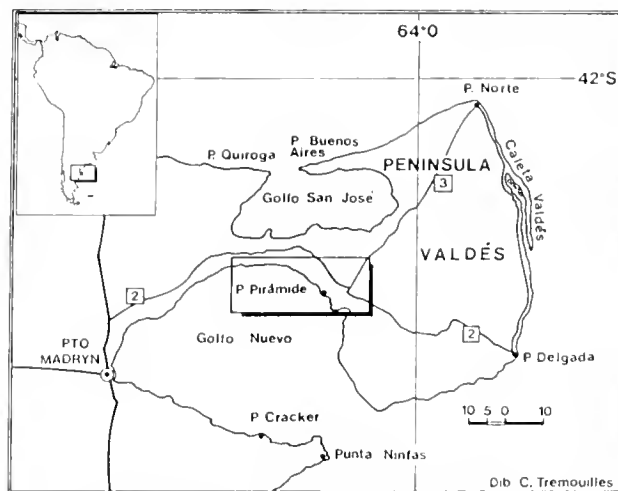
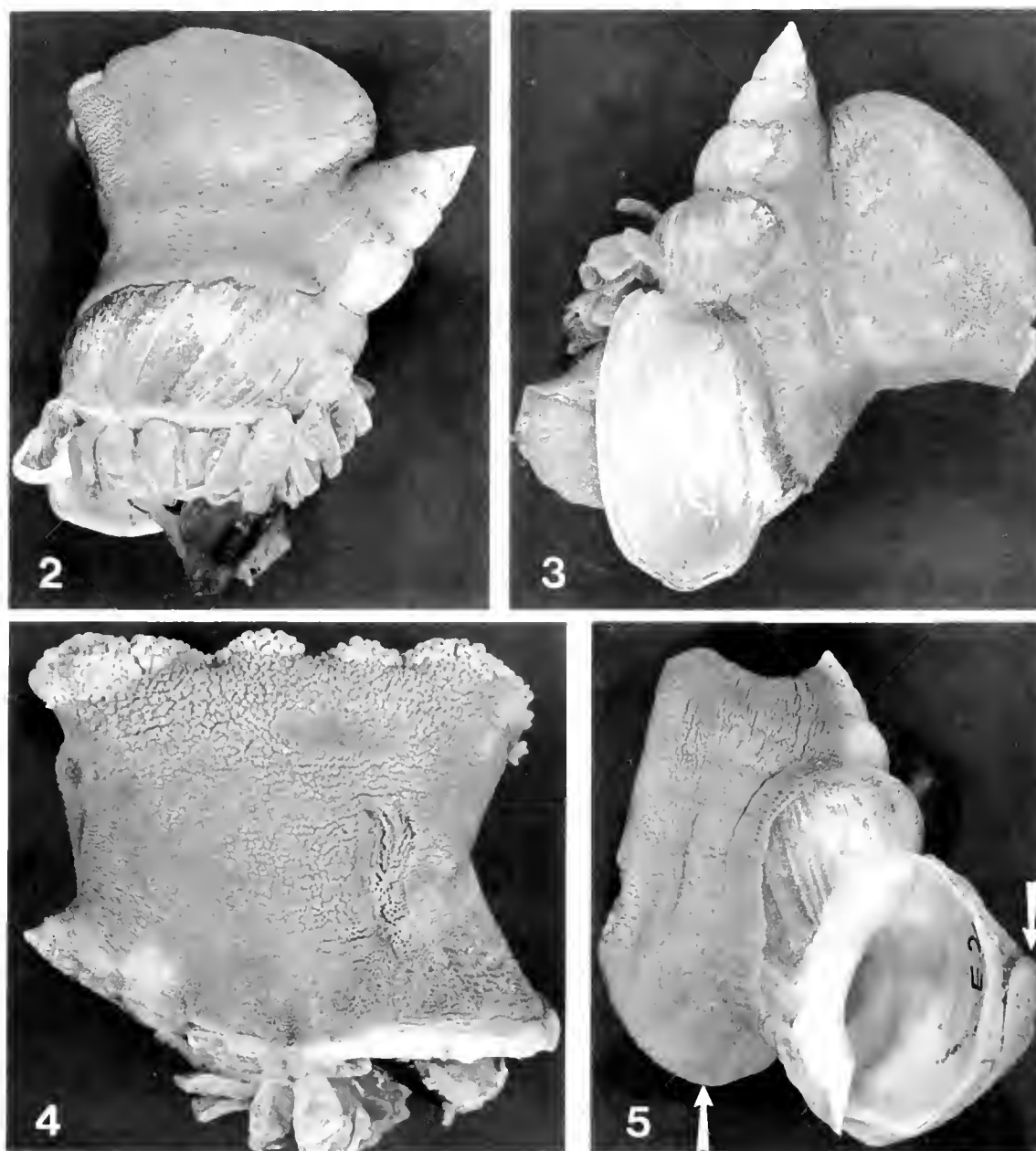


Figure 1. Map of Peninsula Valdés area showing the location of the study area



Figures 2-5. *Buccinanops cochlidium* (Dillwyn) with *Phlyctenanthus australis* Carlgren attached. 1. Oblique apertural view of the gastropod showing egg-capsules attached to the columellar callus. 2. Dorsal view of the same specimen. 3. *P. australis* covering the entire shell of the gastropod. 4. *B. cochlidium* with two anemones attached (arrowheads). All $\times 1$.

Table 1. Bathymetric distribution of *Buccinanops globosum*, *B. cochlidium*, and *Phlyctenanthus australis* at Puerto Pirámide, Argentina

Depth range (m)	5-5.9	6-6.9	8-8.9	9-9.9	10-10.9
No. samples	3	1	1	3	4
Species	<i>B. globosum</i>		<i>B. cochlidium</i>		
Gastropods m ⁻²	28.3	0.60	0.51	0.68	0.49
SD	13.5	0.31	0.35	0.16	0.10
% with one anemone	—	52.35	73.4	67.74	66.6
% with two anemones	—	—	13.3	22.58	20.0
% without anemones	100	17.65	13.3	9.68	13.4

As samples were collected just after the hatching period of *B. globulosum*, their density was probably overestimated. However, *B. globulosum* is always far more abundant than *B. cochlidium*. Of the total gastropods sampled 72.53% had one anemone attached, 13.97% had two. Anemone free specimens comprised only 13.50% of the sample. No correlation between depth and anemone/gastropod density was found.

DISCUSSION

Two species of *Buccinanops*, *B. globulosum* (Kiener, 1834) and *B. cochlidium* (Dillwyn, 1817), inhabit the sublittoral zone near Puerto Pirámide. *Buccinanops globulosum* ranges from the lower midlittoral into the sublittoral to a depth of 6 m below low tide. At depths greater than 6 m it is replaced by *B. cochlidium* (see Table 1). *Buccinanops cochlidium* is the only gastropod that participates in the gastropod-anemone association, although *Phlyctenanthus australis* was also found attached to rocks in the intertidal zone. *Phlyctenanthus australis* was not previously known from south of Mar del Plata. At this locality it may be attached to the decapod *Libinia spinosa* Milne-Edwards, 1834 as noted by Zamponi (1977). Among the other species of gastropods living in the area only *Odontocymbiola magellanica* (Gmelin, 1791) is large enough to be able to carry attached anemones, but *P. australis* is not known to attach itself to the shell of this volutid.

Ross (1974) suggested that one of the possible benefits to the anemone was increased mobility, enabling it to obtain greater amounts of food and also to avoid adverse physiological conditions. The advantages for the gastropod, on the other hand, are not as clear. McLean and Mariscal (1973) and Brooks (1980) suggested that, in the case of the hermit crabs, protection provided by the nematocysts of the anemone would be a benefit. This may also be applicable to *B. cochlidium*. The gastropod apparently is not adversely affected. This may be inferred from the normal reproductive activity, indicated by the egg-capsules attached to the columellar callus of the females (figs. 1, 3).

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Patterns of Diversity and Extinction in Transmarian Muricacean, Buccinacean, and Conacean Gastropods

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ABSTRACT

An analysis of patterns of species-richness in ten muricacean, buccinacean, and conacean families found in the Maryland Miocene formations has uncovered a previously-undetected Serravallian Stage extinction event that decimated the fauna of the Calvertian Subprovince of the Transmarian Province. Prior to the extinction event, the molluscan fauna of the Langhian Stage (Calvert Formation) contained many tropical elements (here referred to as "caloosagenic taxa") that were derivatives of the Miocene Caloosabatchian Province. At the Langhian-Serravallian boundary and the initiation of Choptank deposition, most of the earlier caloosagenic taxa suffered a regional extinction. Breakdown of local ecosystems, probably due to a cooling marine climate, increased toward the end of Choptank time, culminating in the extinction of prominent endemic thaidid and turrid genera. During the latest Serravallian Stage and the beginning of Tortonian time (St. Mary's Formation), the marine climate returned to Langhian conditions and there was an accompanying return to pre-Choptank levels of diversity. The post-Choptank molluscan assemblages differed, however, in containing new caloosagenic taxa, such as *Conus*, and had an extremely reduced thaidid fauna. Several biogeographically important new taxa are also proposed and these include three new genera, *Patuxentrophon* n.gen. (Muricidae: Trophoninae), *Calverturris* n.gen. (Turridae: Mangeliinae), and *Transmariaturris* n.gen. (Turridae: Mangeliinae), and six new species, *Eophorosycon lindajoyceae* n.sp. (Thaididae: Eophorinae), *Buccinofusus patuxentensis* n.sp. (Fasciolaridae), *Busycotypus choptankensis* n.sp., *Turriturris marylandicus* n.sp., and *Turriturris prunicola* n.sp. (all Melongenidae: Busyconinae), and *Calverturris schmidtii* (Turridae: Mangeliinae).

Key words: Extinction, Maryland, Miocene, Transmarian Province.

INTRODUCTION

As a biogeographical entity, the Transmarian Molluscan Province of the northern and central Atlantic Coastal Plain has been relatively unstudied. This early Neogene paratropical province, whose fauna evolved in the Oligocene and became extinct during the Messinian Miocene, has recently been shown to contain numerous endemic gastropod taxa (Petuch, 1988a,b,c). Primary among these are a plethora of distinctive genera in the super-

families Muricacea, Buccinacea, and Conacea, many of which are indicators of the provincial boundaries.

At its height, the Transmarian province extended from the present-day Cape Fear, North Carolina area northward to at least Nova Scotia (figure 46), and encompassed three distinct subprovinces; the southern Pungoian Subprovince, the central Calvertian Subprovince, and the northern Sankatian Subprovince (Petuch, 1988b). The Pungoian Subprovince was centered on the Miocene Albemarle Embayment of North Carolina, while the Calvertian Subprovince had its focus on the diverse biotopes of the Salisbury Embayment of Chesapeake Bay, southern New Jersey, Delaware, Maryland, and northern Virginia. Since the best-preserved and most accessible Transmarian faunas are located along the Patuxent River, the St. Mary's River and the western shore of Chesapeake Bay in Maryland, and since these were the principal faunas used in my provincial analysis, I will deal only with Calvertian taxa in this paper.

In Maryland, the Calvertian Transmarian molluscan fauna is contained within several extremely fossiliferous members of three classic Miocene formations and a possible new formation, the Calvert (contemporaneous with the well-known Kirkwood Formation of New Jersey) (Langhian Stage), the Choptank (early Serravallian Stage), the Little Cove Point Unit (late Serravallian Stage) (the status of this unit is still in debate among authorities; I here follow the nomenclature of Ward and Blackwelder, 1980:D4), and the St. Mary's (latest Serravallian-early Tortonian Stages). Within these formations, a molluscan extinction event, interspersed between two periods of speciation and diversity augmentation, can be recognized within the stratigraphic record and these give insight into possible middle Miocene catastrophic climatic fluctuations along the eastern coast of North America. In this paper, I also hope to shed some light on the higher order diversity patterns of the Transmarian muricacean, buccinacean, and conacean gastropod families. Several important new taxa are also described here in order to fill some nomenclatural gaps in the Calvertian fossil record. These include three new genera, *Patuxentrophon* (Muricidae: Trophoninae), *Calverturris* (Turridae), and *Transmariaturris* (Turridae), and new species of *Ee-*

phorosycon (Thaididae: Ecphorinae), *Buccinofusus* (Fasciolaridae), *Busycotypus* (Melongenidae: Busyconinae), *Turritulur* (Melongenidae: Busyconinae), and *Calverturris* (Turridae). The three superfamilies studied, which include ten families and forty-one genera (listed here in Appendix 1), are excellent indicators of ecosystem collapse during times of extreme climatological stress.

THE TRANSMARIAN GASTROPOD FAUNA

As demonstrated in my earlier work (Petuch, 1988b:11), the Transmarian molluscan fauna represents one of the strangest mixtures of gastropods that can be found anywhere in the fossil record. Unlike any known Recent malacofauna, the Transmarian assemblages contain sympatric suites of both boreal, high arctic gastropod genera such as *Boreotrophon* (Muricidae), *Admete* (Cancellariidae), *Ocnopota* (Turridae), and *Euspira* (Naticidae), and eutropical genera such as *Conus* (Leptocoenidae) (Conidae), *Strioterebrum* (Terebridae), *Lacvityphis* (Muricidae), and *Cymatosyrinx* (Turridae). These arctic and tropical elements coexisted with a large complement of endemic Transmarian genera. Although the Transmarian Province contained taxa from several tropical families, the fauna lacked most of the classic eutropical index groups, such as the Strombidae, Turbinellidae, Cypraeidae, Ovulidae, Cerithiidae, Potamididae, and Lyrriinae (Volutidae) (Petuch, 1988b). Based on the absence of these eutropical elements, the Transmarian province can only be considered to have been a paratropical faunal region.

As determined by Gibson (1967), using foraminiferal assemblages, the marine climate of the Transmarian Province ranged from cool-temperate to temperate, with only a small seasonal fluctuation in water temperature. This climatic stability allowed the evolution of a physiologically stenothermal temperate molluscan fauna, with the endemic genera being unable to live in both the colder boreal conditions to the north and in the warmer tropical conditions of the Miocene Caloosahatchian Province to the south (Petuch, 1988b) (figure 46). The Transmarian arctic and tropical elements represent physiologically eurythermal "invaders" from the Miocene Boreal and Caloosahatchian Provinces. These opportunistic species appear to have evolved physiological tolerations for the warmer (for the boreal taxa) or colder (for the tropical taxa) water conditions of the Transmarian region, and evolved their own endemic Transmarian temperate species complexes.

Transmarian faunal elements that were derived from the tropical Miocene Caloosahatchian Province are here referred to as "caloosagenic". The caloosagenic influence varied through time in the Calvertian Subprovince, with some stages, such as the early Tortonian, containing many tropical taxa and other stages, such as the early Serravallian, containing fewer taxa. Some caloosagens were present only during the Langhian Stage and disappeared from Maryland during the Serravallian Stage, being found subsequently in the fossil beds of Virginia and Florida.

Primary examples of these early Calvertian caloosagens include *Phyllonotus* (*P. millvillensis* (Richards and Harbison, 1942)), *Murexiella* (*M. shilohensis* (Heilprin, 1887)), *Oliva* (*O. harrisi* Martin, 1904), *Amacea* (*A. reticulata* Martin, 1904 and *A. prunicola* Martin, 1904), *Niso* (*N. lineata* (Conrad, 1841)), *Ficus* (*F. harrisi* (Martin, 1904)), and *Architectonica* (*A. trilineatum* (Conrad, 1841)). Other caloosagens make their first appearance in the Calvertian Subprovince at the very end of Salisbury deposition, in the late Serravallian and early Tortonian Stages. Some of these late Calvertian caloosagenic taxa include the previously-mentioned conid genus *Conus* (*Leptocoen* species complex) and the volutacean genus *Mitra* (*M. mariana* Martin, 1904). Still other caloosagenic groups, such as the busyconine genera *Busycotypus* and *Turritulur*, the volutid *Volutifusus*, and the turritellid *Torcula*, existed within the Calvertian area throughout the Langhian, Serravallian, and Tortonian Stages.

Transmarian faunal elements that were derived from the arctic Boreal Province are here referred to as "boreogens". As in the case of the caloosagens, the boreogenic influence also fluctuated through time, being more prevalent in some molluscan assemblages than in others. Unlike the caloosagens, however, very few boreogens were present in the Calvertian Subprovince during the Langhian stage. Of these, only a single genus (the naticid *Euspira*) is known to have ranged throughout the entire Maryland Miocene. The Tortonian Stage, on the other hand, saw the appearance of many new boreogenic taxa that previously had not existed within the Salisbury Embayment. Examples of these later boreal "invaders" include the previously-mentioned genera *Admete* and *Ocnopota*.

DYNAMICS OF TRANSMARIAN DIVERSITY

By recognizing that three separate groups of faunal elements coexisted within the Transmarian Province, the caloosagens, the boreogens, and the Transmarian endemics, it is now possible to undertake a fine-resolution analysis of the diversity patterns of Calvertian Transmarian muricacean, buccinean, and conacean gastropods. These are discussed in the following sections. A listing of all known Calvertian species in these three superfamilies is given in Appendix 2.

Muricacean diversity patterns: Although comprising two families and fourteen genera, the Transmarian muricacean taxa were not distributed equally over time. Only two muricid genera, *Lacvityphis* and *Chesatrophon* (figure 32), and one thaidid genus, *Ecphora* s.s., are temporally distributed throughout the Langhian, Serravallian, and Tortonian Stages. During Langhian time, in the Calvert and Kirkwood (New Jersey) Formations, only two other muricid groups, the caloosagens *Murexiella*, and *Phyllonotus*, are present. The Langhian ecphorine thaidids, on the other hand, underwent a large species

radiation, evolving at least four species of *Ecphora* s.s., at least five species of *Triscephora* (figure 38), two species of *Ecphorosycon*, and two species of *Chesathais* (figure 34) (Petuch, 1989). (Note: The genus *Chesathais*, although possibly arising from a Caloosahatchian stem species (*C. biconicus*), was represented in Maryland by the *C. ecclesiasticus* species complex and can be considered to be an endemic Transmarian radiation.) The large ecphorines apparently dominated the Langhian molluscan assemblages, as their shells are abundant in most units of the Calvert Formation. The small Calvert muricids of the genera *Laevityphis*, *Chesatrophon*, *Murexiella*, and *Patuxentrophon* (figures 1, 2), however, are rare in most assemblages and appear to have occupied the ecological "fringe" areas.

During Serravallian time, the Maryland *Murexiella* species disappeared, (and presumably the New Jersey Kirkwood *Phyllonotus* species), while the caloosagen *Urosalpinx* first made an appearance. This ubiquitous Caloosahatchian ocenebrine taxon survived to become an abundant component of the late Serravallian-Tortonian assemblages of the St. Mary's Formation, and is also extant in the Recent. Also appearing in the early Serravallian was the small muricid *Stephanosalpinx* (figure 31). This distinctive muricean disappeared by the late Serravallian and is confined to the Choptank Formation.

As during the Langhian, the predominant muricean radiation during the early and middle Serravallian time was a complex of ecphorine thaidids. During this time, the genus *Ecphora* s.s. was abundantly represented by at least four species and four stratigraphic subspecies. The subgenus *Triscephora*, although not as species-rich as during Langhian time, was also abundantly represented by two species and at least one stratigraphic subspecies. Likewise, the morphologically-conservative genus *Chesathais* was also present in the Choptank Formation, in this case as a species and two stratigraphic subspecies. Although the primitive genus *Ecphorosycon* was originally thought to have become extinct at the end of Langhian time (Petuch, 1989:43), the recent discovery of a rare Choptank species (*E. lindajoyceae* n.sp., described here) demonstrates that the genus survived into earliest Serravallian time and was part of the rich Choptank ecphorine fauna.

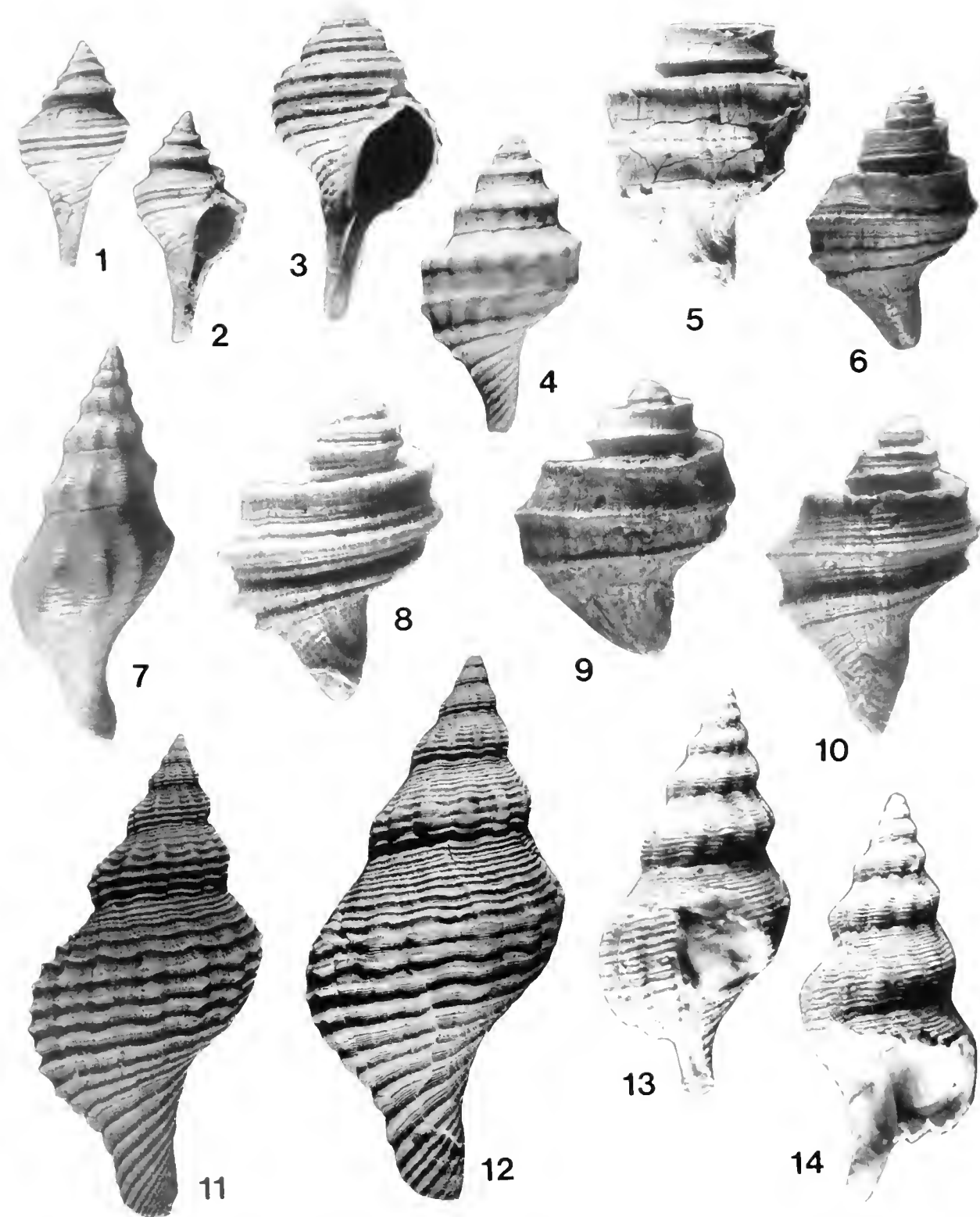
Although ecphorine species diversity declined at the end of Choptank time, muricid diversity increased dramatically at the beginning of Little Cove Point-St. Mary's time (late Serravallian-Tortonian). The abundant presence of the trophonine genera *Chesatrophon* (figure 32), *Boreotrophon*, (figure 29, 30) *Scalaspira* (figure 4), *Lirosoma* (figure 3), and the ocenebrine genera *Urosalpinx* and *Mariasalpinx* (figure 33), particularly underscore this shift toward muricid dominance. This predominance is emphasized even further by the fact that only a single species of *Ecphora* occurs sympatrically with the rich trophonine and ocenebrine faunas found within the various members of the St. Mary's Formation. Although only a single *Ecphora* species is found within any bed of the St. Mary's Formation, these species are much larger than

any ancestral species from the Calvert and Choptank Formations, and are, in fact, the largest muriceans found in the entire Maryland Miocene (*Ecphora gardnerae* Wilson, 1987 often exceeds lengths of 110 mm). This gigantism gave the post-Choptank ecphorine survivors an ecological advantage over their more numerous, but much smaller, muricid cousins—allowing them to utilize large prey items, such as adult specimens of the bivalves *Mercenaria* and *Dosinia*, which were inaccessible to the contemporaneous muricids (Petuch, 1989: 15). Interestingly enough, of all the late Transmarian endemic muricid genera, only *Scalaspira*, *Lirosoma*, and *Boreotrophon* (Transmarian complex) survived into the early Pliocene (Zancian Stage). The last species of these groups, *S. strumosa* (Conrad, 1832), *L. sulcosa* (Conrad, 1830), and *B. tetricus* (Conrad, 1832), respectively, can be found in the Yorktown Formation.

Buccinean diversity patterns: Comprising five families and twelve genera, the Transmarian buccinean gastropods, unlike the muriceans, were more equitably distributed over time. Eight of the twelve genera are found in all three Maryland Miocene formations and are represented by continuous species lineages. Only during St. Mary's time do additional genera appear, and these include the Transmarian endemics *Mariafus* (figure 39), *Pseudaptysis* (figure 35), and *Bulliopsis*. No boreogenic buccinean taxa are known from the Pungoian, Calvertian, or Sankatian Subprovinces.

Of the five Transmarian buccinean families, only the Fascioliariidae showed any appreciable augmentation through time. During Calvert and Choptank time, the family Fascioliariidae was represented by only a single genus, *Buccinofusus* (with two of the species shown here in figures 7, 13, 14). By Little Cove Point-St. Mary's time, however, the number of fascioliariid genera had jumped to three, with the Transmarian endemics *Mariafus* and *Pseudaptysis* possibly representing offshoots that now coexisted with their *Buccinofusus* ancestral stock (Petuch, 1988b). The primitive genus *Buccinofusus*, in particular, underwent rapid evolution, producing three species in the Calvert Formation and one species, each, in the Choptank and St. Mary's Formation and Little Cove Point Unit. Unlike the other Transmarian buccinean families, all the Transmarian fascioliariid genera were endemic to the province, with most taxa being confined to the Salisbury Embayment of the Calvertian Subprovince.

As the complete opposite of the Fascioliariidae, the families Buccinidae and Columbellidae were represented in the Transmarian Province only by caloosagenic genera. The species within these tropically-derived groups, however, represented endemic Transmarian species radiations that paralleled those of their congeners to the south. The genera *Celatoconus*, *Ptychosalpinx*, and *Solenosteira* were all common and prominent components of the Calvert, Choptank, and St. Mary's faunas. In the case of *Ptychosalpinx*, the genus had radiated into an endemic Transmarian species complex with at least



Figures 1-14. Muricid, thaidid, and fascioliid gastropods from the Transmarian Province. 1, 2. *Patuxentrophon patuxentensis* (Martin, 1904), dorsal and ventral views of 18 mm specimen, Zone 17, Choptank Formation, Drum Cliff, St. Mary's County, Maryland. 3. *Lirosoma mariana* Petuch, 1988, holotype, length 27 mm, St. Mary's Formation, St. Mary's River, Maryland. 4. *Scalaspira harasewyehi* Petuch, 1988, holotype, length 13 mm, St. Mary's Formation, St. Mary's River, Maryland. 5. *Ecphorosycon lindajoyceae* new species, holotype, length 55 mm (incomplete), Zone 16, Choptank Formation, Sandgates, St. Mary's County, Maryland, UF 21-466. 6. *Ecphorosycon pamlico* (Wilson, 1987), 68 mm specimen from Zone 10, Calvert Formation, Plum Point,

two sympatric species during St. Mary's time. The Columbellidae, which normally exhibits a high degree of species-richness in eutropical areas, was represented in the paratropical Transmarian Province by only a single genus, *Mitrella*. Although common in all the Maryland Miocene exposures, *Mitrella* never underwent any species radiation and was represented by only two sympatric species in the Calvert Formation and one species, each, in the Choptank and St. Mary's Formations and in the Little Cove Point Unit.

Considering that the overwhelming majority of Transmarian biotopes, as in the Recent Carolinian Province, were composed of soft-bottom sand or mud areas, the family Nassariidae could be expected to be present in the Calvertian region as a large species radiation. Although comprising only two genera, the caloosagenic *Ilyanassa* and the endemic *Bulliopsis*, the Nassariidae dominated many facies of the Calvert and St. Mary's Formations and were the predominant group of small buccinaceans in the Transmarian Province. *Ilyanassa* is present in all Maryland Miocene formations as a series of species swarms, with at least two species in the Calvert Formation, four in the Choptank, and at least three in the St. Mary's. This species-richness is comparable to that seen in the Pliocene, in such formations as the Duplin and Yorktown. The endemic Transmarian genus *Bulliopsis*, on the other hand, is restricted to the Calvertian Subprovince and appears only at the end of Salisbury deposition during Little Cove Point and St. Mary's time.

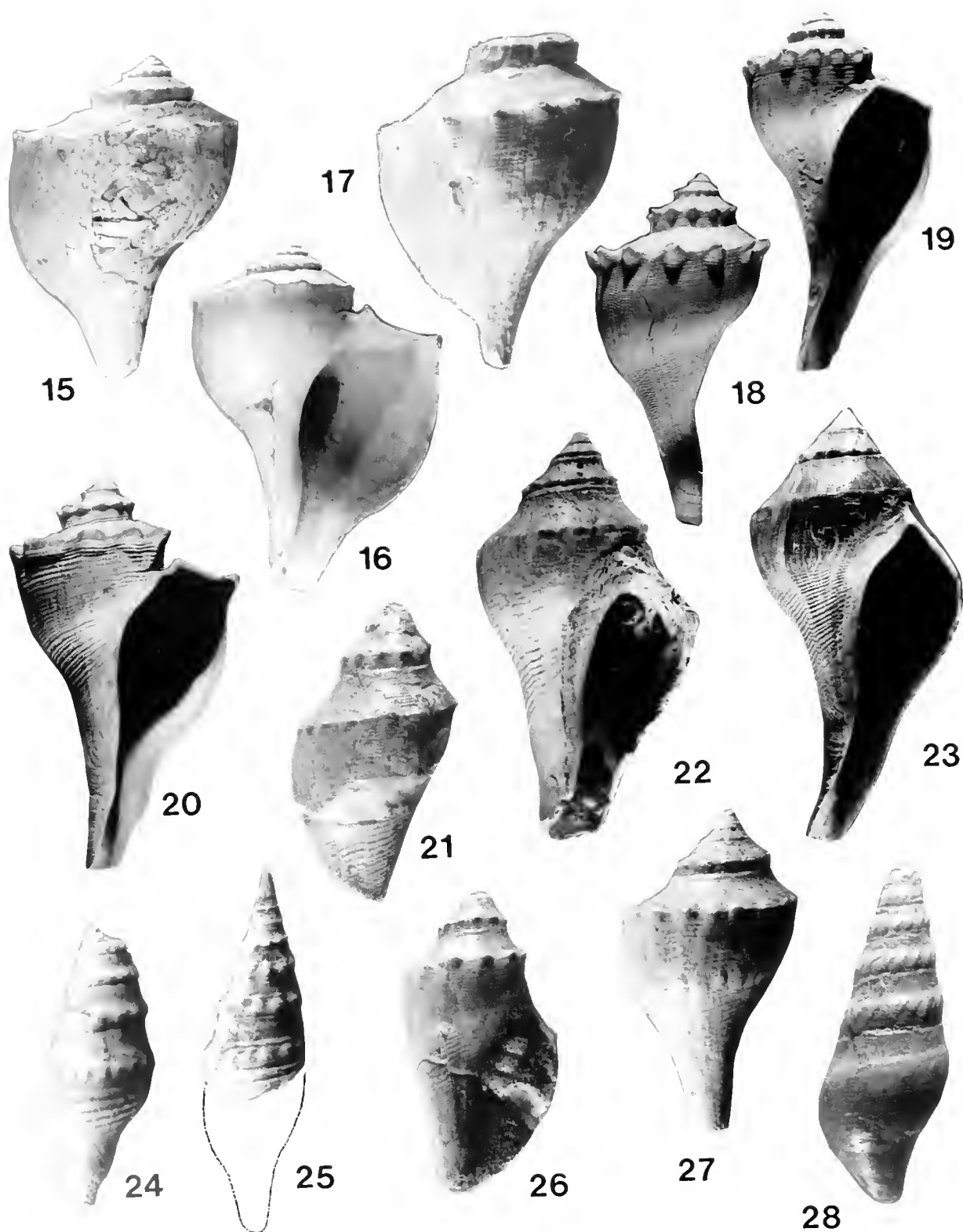
The most extensive macrobuccinean radiation within the Transmarian Province is seen in the busyonine melongenids. These large and abundant predatory gastropods were represented in the Calvertian Subprovince by species swarms in three genera; *Busycotypus* (examples shown here in figures 15–20), *Sycopsis* (figures 36, 37), and *Turritulur* (examples shown here in figures 21–23, 26, 27). These groups are present in all the Maryland Miocene formations and exhibit only gradual morphological shifts through time. *Sycopsis*, the least commonly encountered busyonine, was present in the Transmarian Province as only a single species per formation. The caloosagenic genera *Turritulur* and *Busycotypus*, on the other hand, were often present as sympatric species pairs, and in some cases, such as *Busycotypus* during St. Mary's time, was present as a complex of four species. The species radiations of both of these genera will be discussed in greater detail under the description of new *Busycotypus* and *Turritulur* species in the systematic section at the end of this paper.

Conacean diversity patterns: Of the three Transmarian conacean families, only two, the Turridae and the Terebridae, are temporally distributed throughout the Maryland Miocene and are found in all three formations. The third family, the Conidae, is only known from the St. Mary's Formation and makes its appearance in the Calvertian Subprovince only at the end of Salisbury deposition. Although an abundant and diverse family in the Miocene Caloosahatchian Province, the Conidae was represented in the Transmarian Province by only a single subgenus of *Conus*. This group, *Leptoconus* (figures 40, 41), had evolved into a complex of three endemic sympatric species, *C. diluvianus* Green, 1830, *C. sanctaemariae* Petuch, 1988, and *C. asheri* Petuch, 1989, by the end of St. Mary's time.

The Terebridae, although a common component of all Transmarian molluscan assemblages, was present as only two genera, the caloosagenic *Strioterebrum* and the endemic genus *Laevihastula*. The absence of core tropical terebrids such as *Myurella*, *Hastula*, and *Paraterebra*, which are all found in the Miocene Caloosahatchian and Gatunian Provinces to the south, points to the marginal paratropical nature of the Transmarian Province, and the Calvertian Subprovince in particular. *Strioterebrum* shows an interesting bimodal evolutionary pattern, with two spurts of speciation, one during Calvert time and one at the end of Salisbury deposition, during St. Mary's time. The decline in *Strioterebrum* species-richness during Choptank time may be linked to lower water temperatures during the early Serravallian stage. Unlike *Strioterebrum*, *Laevihastula* is absent in the Calvert Formation but underwent a large species radiation during St. Mary's time, evolving at least four sympatric species.

The third Transmarian conacean family, the Turridae, is present in the Calvertian Subprovince as four subfamilies, twelve genera, and over thirty-five species, making it the single largest toxoglossate radiation in the Maryland Miocene. Of the twelve turrid genera, nine were endemic to the Transmarian Province, two were caloosagenic, and one was boreogenic. The most species-rich subfamily in the Calvertian Subprovince, the Clavinae, comprised three genera; the Transmarian endemics *Chesaclava* (figure 42) and *Sedilopsis*, and the caloosagenic *Cymatosyrinx*. The largest number of species of these genera, particularly *Cymatosyrinx*, is found in the St. Mary's Formation, and this species-richness probably reflects a response to the warmer marine climate during the early Tortonian.

Calvert County, Maryland 7. *Buccinofusus devexus* (Conrad, 1843), 60 mm specimen from Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland 8. *Ecphorosycon kalyx* (Petuch, 1988), 23 mm specimen from Zone 12, Calvert Formation, Scientist's Cliffs, Calvert County, Maryland 9. *Ecphorosycon lindajoyceae* new species, reconstructed paratype, length 69 mm, Zone 16, Choptank Formation, Sandgates, St. Mary's County, Maryland 10. *Ecphorosycon pamlico* (Wilson, 1957), juvenile specimen, length 32 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland 11. *Buccinofusus parilis* (Conrad, 1832), 106 mm specimen from St. Mary's Formation, St. Mary's River, Maryland 12. *Buccinofusus chesapeakensis* Petuch, 1988, holotype, length 93 mm, Little Cove Point Unit, Little Cove Point, Calvert County, Maryland 13. 14. *Buccinofusus patuxentensis* new species, dorsal and ventral views of holotype, length 76 mm, Zone 17, Choptank Formation, Drum Cliff, St. Mary's County, Maryland, UF 21499.



Figures 15–28. *Busyconne* melongenid and turrid gastropods from the Transmarian Province. 15, 16. *Busycotypus choptankensis* new species, dorsal and ventral views of holotype, length 192 mm, Zone 19, Choptank Formation, Drum Cliff, St. Mary's County, Maryland, UF 23798. 17. *Busycotypus calvertensis* Petuch, 1988, dorsal view of holotype, 44 mm (incomplete), Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. 18. *Busycotypus chesapeakeensis* Petuch, 1988, dorsal view of holotype, length 83 mm, Little Cove Point Unit, Little Cove Point, Calvert County, Maryland. 19. *Busycotypus coronatum* (Conrad, 1840), dorsal view of 59 mm specimen, St. Mary's Formation, St. Mary's River, Maryland. 20. *Busycotypus rugosum* (Conrad, 1843), ventral view of 61 mm specimen, St. Mary's Formation, St. Mary's River. 21, 26. *Turritulur marylandicus* new species, dorsal and ventral

In the Maryland Miocene, the subfamily Mangeliinae was represented by the most number of genera, with the Transmarian endemics *Calverturris*, *Mariadrillia*, and *Transmariaturris*, the caloosagen *Glyphostoma*, and the boreogen *Oenopota*. Unlike the Clavinae, the mangeliine turrids were not equally distributed through time, but were divided into two groups: one that was confined to the Calvert and Choptank Formations and the other that appeared only during St. Mary's time. The former group contains *Calverturris* (figures 24, 25), *Transmariaturris* (figure 28), and *Glyphostoma*, all of which disappeared during the mid-Serravallian. The latter group contains only *Mariadrillia*, which is common in the St. Mary's Formation.

The subfamily Turriculinae contained the largest-known Calvertian turrid species radiation, that of the endemic genus *Mariaturricula* (figure 45). This group of large, fusiform conaceans had evolved over seven species during the Maryland Miocene, and these were probably the primary predators on large infaunal polychaetes. The last-known species, *Mariaturricula biscatenaria* (Conrad, 1834), may have competed with the caloosagenic *Leptocoelus* species complex of the St. Mary's Formation. Another endemic Transmarian turriculine group, *Chesasyrinx* (figure 43), is rare in the Calvert and Choptank Formations but is abundant in the St. Mary's Formation, where it evolved into at least two sympatric species. This surge of *Chesasyrinx* evolution may have been in response to the warmer marine climate during St. Mary's time. Coinciding with the early Tortonian speciation acme of *Chesasyrinx* is the appearance of a new turrid group, *Nodisurculina* (figure 44), which is restricted to the St. Mary's Formation.

The subfamily Turrinae, which is characterized by large species radiations and complexes of genera in most Neogene tropical provinces, was poorly represented in the Transmarian Province. Only a single genus, *Hemipleurotoma*, was present, but was equally distributed throughout the entire Maryland Miocene and is found in all three formations. This endemic Transmarian genus is morphologically very conservative, with all known species closely resembling each other. Throughout its temporal range, *Hemipleurotoma* probably occupied the ecological "fringe" area, having had to compete with the extensive vermivorous radiations of the subfamilies Clavinae, Mangeliinae, and Turriculinae. Underscoring this possible competitive exclusion is the fact that only a single *Hemipleurotoma* species is found in each formation, as opposed to the contemporaneous sympatric

species swarms of such successful vermivores as *Sediliopsis*, *Cymatosyrinx*, and *Mariaturricula*.

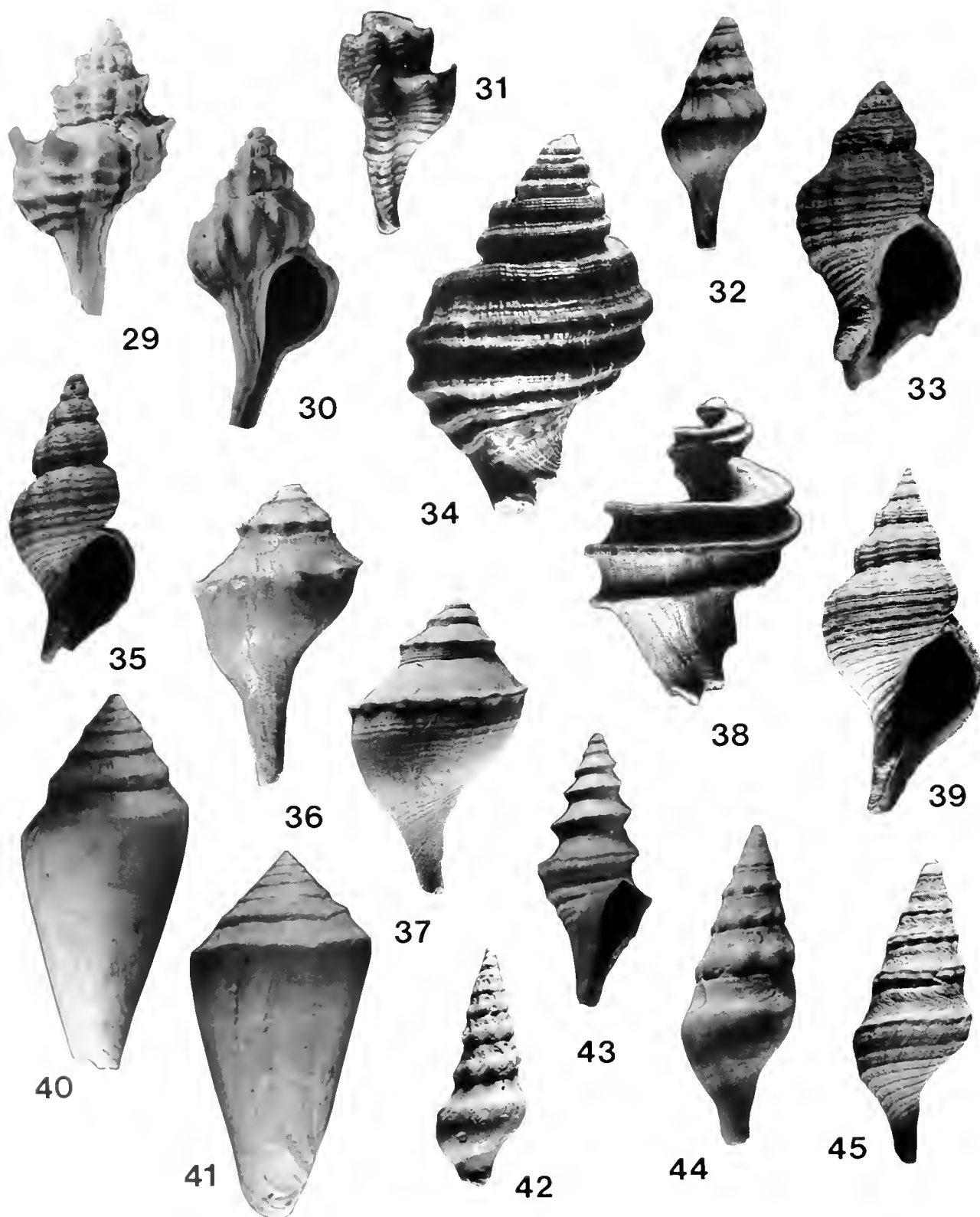
DYNAMICS OF TRANSMARIAN EXTINCTION

Based on both the presence and absence, through time, of caloosagenic and endemic taxa in the Calvertian area, an early Serravallian extinction event can be delineated within the temporal sequence of the Maryland Miocene. This extinction interval began at the initiation of Choptank deposition, at the boundary of Planktonic Foraminifer Zones N10–N11 and N12 (Gibson, 1983:38), and reached a peak at the end of Choptank deposition, at the boundary of Planktonic Foraminifer Zones N12 and N13. During this time, which ranges from 13 million years B.P. to approximately 12.3 million years B.P. (Gibson, 1983: fig. 2), several dominant gastropod groups disappeared from the Transmarian ecosystems, resulting in post-Choptank molluscan assemblages that differed in appearance from those of Langhian age.

Since eutropical caloosagenic taxa such as *Glyphostoma*, *Oliva*, *Niso*, *Ficus*, and *Architectonica* disappeared at the end of Calvert time, but boreogenic taxa such as *Oenopota* and *Euspira* persisted throughout Choptank time, it can be assumed that a climatic cooling event was the primary culprit in the extinction of the dominant Langhian Transmarian gastropod taxa. As pointed out by Stanley (1986), a "refrigeration" event, such as the Serravallian cooling episode, is most probably the cause of both regional and mass extinctions of neritic faunas throughout the Phanerozoic. Since many of the typical Transmarian endemic genera, such as *Chesatrophon*, *Buccinofusus*, *Sycopsis*, *Chesaclava*, and *Mariaturricula*, survived the Serravallian extinction and are present in the subsequent St. Mary's Formation, the Choptank-aged refrigeration event was not as severe as that of the mass extinction episode during the late Tortonian and Messinian Stages (the "Transmarian Extinction" of Petuch, 1988b:12). During that late Miocene time, over 95% of the Transmarian gastropod species lineages disappeared. The Serravallian extinction episode, then, may have been a precursor to the catastrophic Transmarian Extinction of two million years later. The reduction of muricean, buccinean, and conacean species-richness during Choptank time is shown, graphically, in figure 47.

Although not totally devastating to Transmarian gastropod assemblages, the Serravallian extinction was apparently severe enough to cause the extinction of tem-

← views of holotype, length (incomplete) 60 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland, UF 21467. **22.** *Turrifugur turriculus* Petuch, 1988, holotype, length 32 mm, St. Mary's Formation, St. Mary's River. **23.** *Turrifugur fusiforme* (Conrad, 1840), 69 mm specimen, St. Mary's Formation, St. Mary's River. **24.** *Calverturris bellacrenata* (Conrad, 1841), 28 mm specimen, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. **25.** *Calverturris schmidtii* new species, dorsal view of incomplete holotype (outline reconstructed), length 23 mm, Zone 17, Choptank Formation at Drum Cliff, St. Mary's County, Maryland, UF 21500. **27.** *Turrifugur prunicola* new species, dorsal view of holotype, length 35 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland, UF 21468. **28.** *Transmariaturris calvertensis* (Martin, 1904), dorsal view of 40 mm specimen, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland.



Figures 29–45. Representative species of endemic Transmarian gastropod genera and endemic species complexes. 29. *Boreotrophon lindae* Petuch, 1985, length 13 mm, St. Mary's Formation (*Boreotrophon* Fischer, 1884, Transmarian species complex). 30. *Boreotrophon harasevychi* Petuch, 1985, length 16 mm, St. Mary's Formation (*Boreotrophon* Fischer, 1884, Transmarian species complex). 31. *Stephanosalpinx candelabra* Petuch, 1985, length 18 mm, Choptank Formation, lateral view showing small labial tooth (*Stephanosalpinx* Petuch, 1958). 32. *Chesatrophon chesapeakeanus* (Martin, 1904), length 11 mm, St. Mary's Formation (*Chesatrophon* Petuch, 1955). 33. *Mariasalpinx emilyae* Petuch, 1985, length 28 mm, St. Mary's Formation (*Mariasalpinx* Petuch,

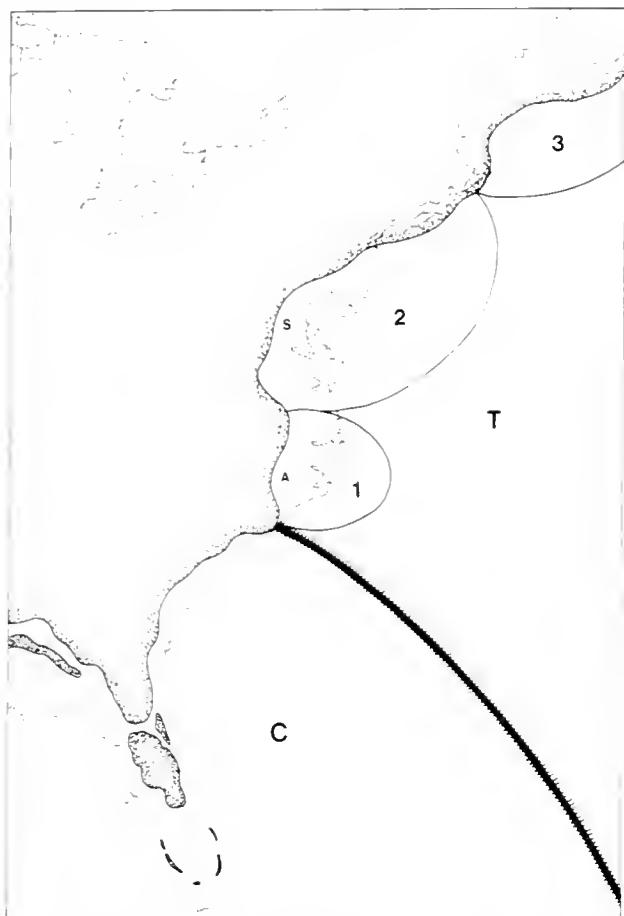


Figure 46. Miocene eastern North America, showing continental configuration (stippled area) and molluscan faunal provinces, superimposed upon the outline of Recent North America (dotted line). C = Miocene Caloosahatchian Molluscan Province. T = Transmarian Province, with its three subprovinces, the Pungoian (1), the Calvertian (2), and the Sankatian (3); thick fence-line represents the boundary between the Transmarian and Miocene Caloosahatchian Provinces. S = Salisbury Embayment, A = Albemarle Embayment

perature-sensitive organisms such as the Transmarian *Nautilus* species (Martin, 1904:130), the Transmarian archeocetian whales of the genera *Priscodelphinus* Cope, 1868, *Ixacanthus* Cope, 1890, *Cetophis* Cope, 1868, and *Delphinodon* Leidy, 1869, and the porpoise genus *Oryc-*

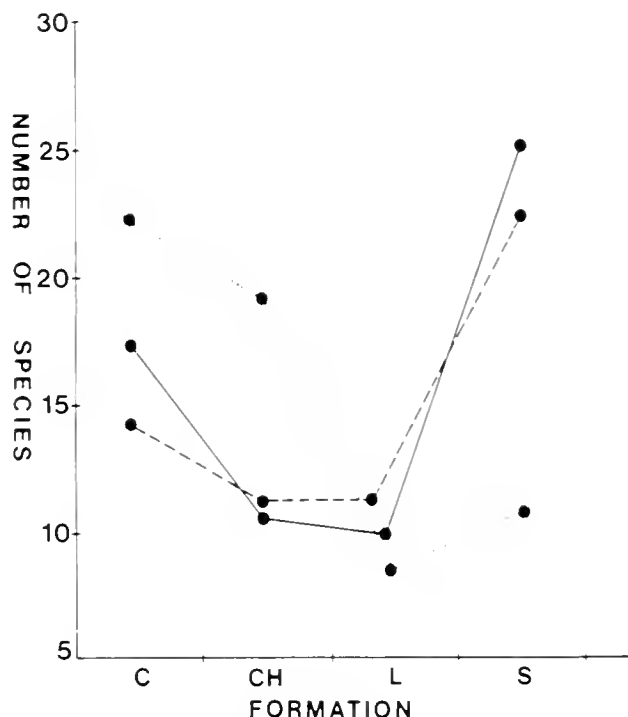


Figure 47. Species-richness of Calvertian Transmarian muricean, buccinean, and conacean gastropods during the middle Miocene, showing drop in diversity during Choptank-Little Cove Point time. Dotted line = number of known muriceans; dashed line = number of known buccineans; solid line = number of known conaceans. Calvertian formations include the Calvert (C), Choptank (CH), Little Cove Point Unit (L), and St. Mary's (S). Numbers of species per superfamily are taken from the data listed in Appendix 2

terocetus Cope, 1867 (Case, 1904). These last mentioned cetacean genera disappeared abruptly at the end of Calvert deposition, contemporaneously with the disappearance of the caloosagenic gastropod genera *Glyphostoma*, *Niso*, *Oliva*, and *Ficus*. Besides the endemic cetaceans, a large fauna of other Transmarian vertebrates died out at the Langhian-Serravallian boundary. Included are the giant endemic stingray *Raja dux* Cope, 1867, the *Myllobatus gigas* Cope, 1867—*M. pachydon* Cope, 1867 complex of rays, the giant carchariid sharks *Carcharias collata* Case, 1904, *C. laevis* (Cope, 1867), *C. mag-*

1985). **34.** *Chesathais lindae* Petuch, 1955, length 50 mm, Choptank Formation (*Chesathais* Petuch, 1955). **35.** *Pseudaptyxis sanctaemariae* Petuch, 1955, length 26 mm, St. Mary's Formation (*Pseudaptyxis* Petuch, 1955). **36.** *Sycopsis lindae* Petuch, 1955, length 65 mm, Choptank Formation (*Sycopsis* Conrad, 1867). **37.** *Sycopsis tuberculatum* (Conrad, 1840), length 52 mm, St. Mary's Formation (*Sycopsis* Conrad, 1867). **38.** *Ecphora* (*Trisecephora*) *eccentrica* Petuch, 1959, length 55 mm, Calvert Formation (*Trisecephora* Petuch, 1955, subgenus of *Ecphora* Conrad, 1843). **39.** *Mariafusius marylandicus* (Martin, 1904), length 60 mm, St. Mary's Formation (*Mariafusius* Petuch, 1955). **40.** *Conus* (*Leptoconus*) *asheri* Petuch, 1955, length 42 mm, St. Mary's Formation (*Leptoconus* Swainson, 1840, subgenus of *Conus* Linnaeus, 1755, Transmarian species complex). **41.** *Conus* (*Leptoconus*) *diluvianus* Green, 1830, length 63 mm, St. Mary's Formation (*Leptoconus* Swainson, 1840, subgenus of *Conus* Linnaeus, 1755, Transmarian species complex). **42.** *Chesaclava quarlesi* Petuch, 1955, length 14 mm, St. Mary's Formation (*Chesaclava* Petuch, 1955). **43.** *Chesasyrinx rotifera* (Conrad, 1830), length 24 mm, St. Mary's Formation (Conrad, 1862), length 14 mm, St. Mary's Formation (*Nodisurculina* Petuch, 1955). **45.** *Mariaturricula biscatenaria* (Conrad, 1834), length 35 mm, St. Mary's Formation (*Mariaturricula* Petuch, 1955).

na (Cope, 1867), and *C. incidens* Case, 1904, and the giant manatee *Trichechus giganteus* (DeKay, 1842) (Case, 1904). It seems noteworthy that the Calvert-Choptank molluscan extinction correlates with the impressive mammalian and elasmobranch extinctions, indicating that there was a province-wide catastrophic event that affected many animal groups.

After the initial Langhian-Serravallian boundary refrigeration event, there was a gradual and further climatic deterioration during Choptank time. This gradualistic pattern is demonstrated by the sequential extinction of several taxa. Victims of the initial Langhian-Serravallian boundary event were the caloosagenic, eutropical muricid genera *Murexiella* and *Phyllonotus*, which disappeared at the end of Calvert-Kirkwood time. These thermophilic genera, which are widespread in the Recent eutropical Caribbean Province (Petuch, 1987), would have been particularly sensitive to lowered water temperature. Another caloosagenic muricid genus, *Laevityphis*, was extremely rare in the Choptank Formation, possibly indicating a sensitivity to cooler temperatures and a marginal survival ability. Likewise, the ecphorine thaidid subgenus *Trisecphora*, which had previously undergone a large species radiation in the Calvert Formation, was present during Serravallian time only as a single species per stratigraphic unit. This drop in *Trisecphora* species richness may also have been in response to lower water temperatures.

Of particular interest is the thaidid genus *Ecphorosycon*, which appeared to have its center of speciation in the warmer southern Pungoian Subprovince (Petuch, 1989). This distinctive Transmarian endemic survived into the very beginning of Choptank deposition (Zone 16) as a single Calvertian species, but became extinct before the deposition of the upper bed of the Drum Cliff Member (Zone 17). This ephemeral existence of the thermophilic genus *Ecphorosycon* also points to a cooling event during earliest Serravallian time. The possibly more cool-tolerant genus *Ecphora* s.s., however, proliferated into several species complexes during Choptank time and this accounts for the lag in muricacean extinction seen in figure 47. Climatic conditions apparently deteriorated so greatly by the end of Serravallian time, however, that even less thermophilic genera such as *Ecphora* s.s., *Chesathais*, and *Trisecphora* declined in species richness. At the end of Choptank deposition, the latter two thaidid genera and all but one complex of *Ecphora* s.s. became extinct, underscoring the ecological impact of the cooling event. In the overlying Little Cove Point Unit (late Serravallian Stage), only one, or possibly two, species of *Ecphora* s.s. are known to exist; a feeble "ghost" of the large Calvert and Choptank ecphorine radiations.

The turrid genera *Calverturris* and *Transmariaturris* and the trophonine genus *Patuxentrophon* also disappeared during late Choptank time, along with *Ecphorosycon*, *Chesathais* and *Trisecphora*. The simultaneous loss of these stenothermal temperate endemics could only have been produced by a refrigeration catastrophe. Interestingly enough, the large Calvertian trophonine ra-

diation, which appears in the subprovince only at the end of the Serravallian refrigeration event, may have been a left-over of a boreal invasion during the coldest time, at the Choptank-Little Cove Point Unit boundary. This strong post-Choptank boreogenic influence, which includes *Boreotrophon* and *Scalaspira*, may have represented physiological adaptations to warmer water conditions during Little Cove Point-St. Mary's time.

SYSTEMATICS

The type material of the following new species is deposited in the invertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and bears UF numbers.

Order Caenogastropoda

Superfamily Muricea

Family Thaididae

Subfamily Ecphorinae Petuch, 1988

Genus *Ecphorosycon* Petuch, 1988

Ecphorosycon lindajoyceae new species
(figures 5, 9)

Material examined: HOLOTYPE—length 55 mm (incomplete), in basal bed (Zone 16) of Choptank Formation, along waterline of Patuxent River at Sandgates, St. Mary's County, Maryland, UF21466; PARATYPE—length 69 mm (reconstructed with plasticine clay), same locality as holotype, collection of author.

Description: Shell inflated, with globose body whorl and distinctly pyriform outline; spire protracted, scalariform; shoulder sloping; subsutural area flattened, producing stepped spire whorls; body whorl ornamented with 3 rounded, thin, low, adherent cords; cord along shoulder of body whorl projecting upward (posteriorward), becoming progressively more bladelike on earlier whorls; entire body whorl, spire whorls, and siphonal canal sculptured with spiral threads; spiral threads give entire shell silky texture; spire whorls ornamented with 2 thin cords, with cord along shoulder being bladelike in form; siphonal canal proportionally short and broad for genus; umbilicus wide, flaring, well developed.

Etymology: Named for my wife, Linda Joyce Petuch, who assisted me with my collecting along the St. Mary's River and Chesapeake Bay.

Discussion: Previously (Petuch, 1989:43) I had stated that the genus *Ecphorosycon* had become extinct at the end of Langhian time, in the upper beds of the Calvert Formation. The discovery of an *Ecphorosycon* species in the lowest bed of the Choptank Formation (Zone 16), however, demonstrates that the genus survived into early Serravallian time. Within Zone 16, the last surviving *Ecphorosycon*, *E. lindajoyceae*, is rare, with only a few fragmentary specimens having ever been collected. The new species has never, to my knowledge, been collected in the upper Choptank beds (Zones 17, 18, and 19), whose faunas have been relatively well-studied. The absence of

this large and distinctive ephorine from Zone 17 indicates that *Ecphorosycon* became extinct in earliest Serravallian time, making it an excellent index fossil for Zone 16.

Ecphorosycon lindajoyceae is most similar to *E. pamlico* (Wilson, 1987) from Zone 10 of the Plum Point Member of the Calvert Formation and from the Bonerton Member of the Pungo River Formation of North Carolina. The new species differs from *E. pamlico* (figure 6, 10) in being a much wider, much more inflated shell with a wider, stumper, less elongated siphonal canal. The spire of *E. pamlico* is higher and much more protracted than the spire of *E. lindajoyceae*, which is distinctly lower and depressed. The spiral threads on the spire, body whorl, and siphonal canal of the new species are also much finer than those of the coarsely-sculptured *E. pamlico*. The new species is also quite different from *E. kalyx* (Petuch, 1988) from Zones 12 and 14 of the Plum Point Member of the Calvert Formation (figure 8), and differs in being a much more inflated, globose shell, in having reduced, less developed cords, and in having a sculpture pattern of fine spiral threads.

The preservation of shells within Zone 16 is poor, with almost every specimen being collected in a fragmentary state. The paratype of *E. lindajoyceae* (figure 9) was actually flattened by the pressure of sedimentary compaction and was collected, piecemeal, as a handful of fragments. These were later reassembled over a template of plasticine clay. The holotype is the best, most complete, specimen found to date. Although fragmentary, the holotype exhibits enough salient characteristics to allow for easy separation from the older *E. pamlico* and *E. kalyx*. At the type locality, Sandgates on the Patuxent River in Zone 16 of the Choptank Formation, *Ecphorosycon lindajoyceae* co-occurs with a large ephorine fauna, including *Ephora* (*Ecphora*) *meganæ sandgatesensis* Petuch, 1989, *E. (Ecphora) rikeri harasewyci* Petuch, 1989, *E. (Ecphora) choptankensis vokesi* Petuch, 1989, *Ecphora (Trisecephora) smithae* Petuch, 1988, and *Chesathais lindae donaldasheri* Petuch, 1989.

Family Muricidae

Subfamily Trophoninae Cossmann, 1903

Genus *Patuxentrophon* new genus

Diagnosis: Shell vase-shaped, with sharply angled, carinated shoulder and high, distinctly scalariform spire; body whorl wide and inflated, tapering rapidly anteriorly into siphonal canal; siphonal canal long, slender, straight, equal in length to body whorl; body whorl ornamented with 10 large, rounded cords; smaller, secondary cords often present between larger, primary cords; shoulder cord largest; spire whorls ornamented with 5 cords; siphonal canal ornamented with 15–20 large, rounded cords; aperture oval.

Type species: *Chrysodomus patuxentensis* Martin, 1904, Choptank Formation, Serravallian Miocene of Maryland (figures 1, 2).

Other species in *Patuxentrophon*: *Patuxentrophon* unnamed species, Zone 10 of the Plum Point Member of the Calvert Formation.

Etymology: A combination of “Patuxent”, for the Patuxent River of Maryland, and the muricid genus *Trophon*.

Discussion: Martin (1904:184) referred this small muricid group to the archaic neptuniid genus *Chrysodomus* Swainson, 1852, primarily on the basis of a similarity in ribbed sculpture patterns. *Patuxentrophon*, however, differs from neptuniids in being a much tinier shell with a proportionally much longer and much better developed siphonal canal. The new genus is distinctly trophonine, having the same general size, siphonal canal development, and spiral sculpture pattern as living *Boreotrophon* species such as the Oregonian *B. disparilis* (Dall, 1891) and living *Trophonopsis* species such as the Alaskan *T. kamchatkanus* (Dall, 1902). *Patuxentrophon* also shares many characteristics with the late Serravallian, Tortonian, and Messinian trophonine genera *Lirosoma* Conrad, 1862 (figure 3), and *Scalaspira* Conrad, 1862 (figure 4), having the sculpture of the former and the shape of the latter. It is possible that the Langhian–early Serravallian *Patuxentrophon* represents the stem-stock from which the later Miocene *Lirosoma* and *Scalaspira* evolved.

Superfamily Buccinacea

Family Fascioliariidae

Subfamily Fascioliariinae Gray, 1853

Genus *Buccinofusus* Conrad, 1868

Buccinofusus patuxentensis new species (figures 13, 14)

Material examined: HOLOTYPE—Length 77 mm, from Zone 17, Drum Cliff Member of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, Patuxent River, UF 21499; PARATYPE—length 54 mm, same locality as holotype, collection of author.

Description: Shell elongately fusiform, with very elevated, protracted spire; subsutural area sloping, shoulder rounded; shoulder and middle section of body whorl ornamented with 10–12 low, axially-arranged riblike knobs; spire whorls with 8–12 riblike knobs bordering suture; entire shell, in turn, sculptured with extremely numerous fine spiral cords and threads; cords finest along subsutural area, becoming coarser on midbody, and coarsest on siphonal canal; siphonal canal well developed, short in proportion to length of spire.

Etymology: Named for the Patuxent River, which borders the type locality.

Discussion: *Buccinofusus patuxentensis* occupies the evolutionary midpoint between the primitive *B. devexus* (Conrad, 1843) of the Calvert Formation (figure 7) and the more advanced *B. chesapeakeensis* Petuch, 1988 of the Little Cove Point Unit (figure 12) and *B. parilis*

(Conrad, 1832) of the St. Mary's Formation (figure 11). Morphologically, *B. patuxentensis* resembles the slender and proportionally higher-spined *B. devexus* in shape, but shares the coarser spiral sculpture of *B. chesapeakeensis*. Of the known *Buccinofusus* species, *B. patuxentensis* is closest to the Little Cove Point *B. chesapeakeensis*, but differs in having finer and more numerous spiral cords on the body whorl and spire, and in having stronger and more numerous knobs on the spire whorls.

Through time, from the Langhian to the Tortonian, the genus *Buccinofusus* underwent parallel shifts in two morphological characters; shell length-width ratio and degree of sculpture coarseness. The oldest species, *B. devexus*, is the most slender and is only faintly sculpted with fine spiral threads. The Choptank *B. patuxentensis* retains the slender shape of *B. devexus* but presages the heavier sculptural pattern of the later forms. The Little Cove Point *B. chesapeakeensis* retains the sloping shoulder and fine sculpturing on the subsutural area, as seen in the earlier species, but has the inflated body whorl and coarse, widely-spaced cords around the midbody and siphonal canal that typify the advanced forms. This characteristic Transmarian lineage culminates in the St. Mary's *B. parilis*, which has the most inflated body whorl, lowest spire, and uniformly coarse sculpture over the entire shell.

Family Melongenidae

Subfamily Busyconinae Finlay and Marwick, 1937

Genus *Busycotypus* Wenz, 1943

Busycotypus choptankensis new species
(figures 15, 16)

Material examined: HOLOTYPE—Length 192 mm (incomplete), in Zone 19 of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, along Patuxent River, UF 21498.

Description: Shell vase-shaped, very inflated, with ovately-cylindrical body whorl; shoulder very broad, wider than length of body whorl; shoulder sharply angled, carinated, ornamented with 16–20 low, undulating knobs per whorl; spire low, stepped; sutural area with wide, deep, flat-bottomed sulcus, producing widely canaliculate spire whorls; periphery of sutural sulcus bordered with large, rounded, undulating cord; body whorl ornamented with longitudinal growth lines, devoid of spiral sculpture; spire whorls ornamented with 6–8 faint spiral threads; siphonal canal broad, ornamented with 10–12 low, nearly obsolete spiral cords; aperture extremely wide, open, flaring, with smooth, unornamented interior; parietal area glazed.

Etymology: Named for the Choptank Formation, for which this new species is an index fossil.

Discussion: As in the case of *Buccinofusus patuxentensis*, *Busycotypus choptankensis* fills in a gap in the evolutionary record of the Maryland Miocene *Busycotypus* lineage. The new species is closest to *B. chesa-*

peakensis Petuch, 1988 (figure 18) of the younger Little Cove Point Unit, especially in being a smooth, unornamented shell with low, undulating shoulder coronations. The Choptank ancestor differs from its Little Cove Point descendant, however, in being a much more inflated shell, by being proportionally thinner and more fragile, and in having less developed, lower coronations on the shoulder and spire whorls. Of the two related St. Mary's species, *B. coronatum* (Conrad, 1840) (figure 19) and *B. rugosum* (Conrad, 1843) (figure 20), *B. choptankensis* is most similar to the latter, but differs in having lower, less developed coronations and in lacking the heavy spiral corded sculpture that characterizes *B. rugosum*. From the small, ancestral *B. calvertensis* Petuch, 1988 (figure 17), *B. choptankensis* differs in being a smooth, unsculptured shell with a much better developed, wider canaliculate suture.

Through time, the Transmarian coronated *Busycotypus* species exhibited three morphological trends; becoming proportionally less inflated, developing wider and deeper sutural sulci, and developing larger and more prominent shoulder and spire coronations. The primitive *B. calvertensis* is a very wide, inflated shell with small coronations and a tiny, almost nonexistent sutural canal. *Busycotypus choptankensis* retains the inflated shell shape of the ancestral *B. calvertensis*, but has large, well defined shoulder coronations, and has a very well developed, wide sutural canal. The next youngest in the sequence, *B. chesapeakeensis*, has a wide sutural canal like *B. choptankensis* but has even larger, better defined shoulder coronations. Unlike the primitive species *B. calvertensis* and *B. choptankensis*, however, *B. chesapeakeensis* has the slender, more attenuated body form of the advanced species. The two St. Mary's species, *B. coronatum* and *B. rugosum*, both appear to have evolved from the Little Cove Point *B. chesapeakeensis*, and share the same attenuated body form. *Busycotypus coronatum* retains the smooth, unsculptured body whorl of *B. choptankensis* and *B. chesapeakeensis*, but has the largest, most pronounced shoulder coronations of the whole complex. The contemporaneous and sympatric *B. rugosum*, on the other hand, has a heavily sculptured, corded body whorl and large, rounded, knoblike shoulder coronations. The noncoronated *Busycotypus* species from the St. Mary's Formation, *B. asheri* Petuch, 1988, and *B. alveatum* (Conrad, 1863), appear to belong to a separate species complex and are not closely related to the coronated forms.

Genus *Turrifulgur* Petuch, 1988

Turrifulgur marylandicus new species
(figures 21, 26)

Material examined: HOLOTYPE—Length (incomplete) 60 mm, in Zone 10, Plum Point Member of Calvert Formation, at Plum Point, Calvert County, Maryland, UF21467.

Description: Shell elongated, cylindrical in form, with

high, protracted spire; shoulder sharply angled, low on body whorl, below wide, very sloping subsutural area; shoulder ornamented with 12 evenly-spaced, small, sharply-pointed knobs; spire whorl ornamented with 12 knobs per whorl; siphonal canal (missing on holotype) elongated and slender (extrapolated from holotype); body whorl sculptured with numerous fine spiral threads, which become nearly obsolete around mid-body; sloping subsutural area sculptured with 12 large spiral threads; siphonal canal sculptured with numerous large, evenly-spaced spiral cords; aperture proportionally narrow.

Etymology: Named for the State of Maryland.

Discussion: The elongate, high-spined *Turritulur marylandicus* stands out as unique among the known Transmarian *Turritulur* species. The extremely attenuated body form is reminiscent of *T. atraktoides* (Gardner, 1944) from the late Burdigalian Oak Grove Formation of northern Florida, and the Langhian *T. marylandicus* appears to belong to the same species complex. The new Maryland busyconine, however, differs from the older Oak Grove species in being an even more-elongated shell with a more drawn-out body whorl, in having a more protracted, scalariform spire, and in having a much more sloping shoulder and subsutural area. *Turritulur marylandicus* also has fewer knobs per whorl on the spire than does its more finely-ornamented Caloosahatchian relative.

This new protracted Transmarian *Turritulur* is sympatric with *T. prunicola* n.sp. (described in the next section) at Plum Point. *Turritulur marylandicus* differs from this congener in being a larger, more elongated shell with a much higher spire. The presence of two sympatric species of *Turritulur* in the Calvert Formation reflects a similar pattern seen in the early Langhian Shoal River Formation of northern Florida, where two species, *T. aldrichi* (Gardner, 1944) and *T. dasum* (Gardner, 1944), also co-occur.

Turritulur prunicola new species
(figure 27)

Material examined: HOLOTYPE—Length 35 mm, in Zone 10, Plum Point Member of Calvert Formation, at Plum Point Calvert County, Maryland, UF21468.

Description: Shell vase-shaped, fusiform, with sharply-angled shoulder; spire slightly stepped, comparatively low and flattened for genus; subsutural area only slightly flattened, subplanar; shoulder of body whorl ornamented with 14 small, low, evenly-spaced knobs; spire whorls ornamented with 14 small knobs per whorl; body whorl pinching-in abruptly to base of siphonal canal; siphonal canal slender, narrow; body whorl, siphonal canal, spire whorls and subsutural area sculptured with numerous very fine spiral threads, giving shell silky appearance; aperture oval.

Etymology: Named for Plum Point, Calvert County, Maryland, the type locality.

Discussion: Although sympatric with *Turritulur marylandicus* in Zone 10, *T. prunicola* belongs to a separate species lineage. The narrow *T. marylandicus* appears to be a member of the *T. atraktoides* (Gardner, 1944)–*T. dasum* (Gardner, 1944) species complex, while *T. prunicola* probably belongs to the *T. aldrichi* (Gardner, 1944) species complex. Both Calvert species are caloosagenic offshoots of these contemporaneous complexes. Although the *T. prunicola* lineage survived until the Tortonian Stage (as *T. fusiforme* (Conrad, 1840) and *T. turriculus* Petuch, 1988), the *T. marylandicus* lineage died off during the Langhian Stage, and is not found in the upper beds of the Calvert Formation nor in the Choptank Formation.

Turritulur prunicola is closest in general shell morphology to *T. turriculus* Petuch, 1988 (figure 22) from the Windmill Point Member of the St. Mary's Formation. The new species differs from its St. Mary's descendant in having a much lower spire, in having fewer and smaller knobs on the shoulder and spire whorls, and in having finer and more delicate spiral threaded sculpture. *Turritulur prunicola* is also similar to *T. fusiforme* (Conrad, 1840) (figure 23) from Zone 24 of the St. Mary's Formation, but differs in being a smaller shell with a more sharply angled shoulder and proportionally lower spire.

Superfamily Conacea

Family Turridae

Subfamily Mangeliinae Fischer, 1887

Genus *Calverturris* new genus

Diagnosis: Shells elongately fusiform, with high, protracted spires and extended, slender siphonal canals; shoulders subcarinated, ornamented with nodulose cord below greatly sloping subsutural area; nodulose cord borders suture on spire whorls; body whorls ornamented with 6–8 large, evenly-spaced spiral cords; fine spiral threads present between cords of some species; siphonal canals ornamented with numerous spiral threads; anal notch shallow, with greatest indentation corresponding to nodulose shoulder cord; protoconchs proportionally small, rounded, domelike, composed of one and one-half whorls; apertures narrow.

Type species: *Pleurotoma bellacrenata* Conrad, 1841, Calvert Formation, Langhian Miocene of Maryland (figure 24).

Other species in *Calverturris*: *Calverturris schmidtii* n.sp., Choptank Formation, Serravallian Miocene of Maryland, described here.

Etymology: A composite of “*Calvert*”, for the Calvert Cliffs of Maryland, and “*turris*”, “tower”.

Discussion: This small group of Transmarian turrids is one of the most morphologically-distinctive of the known Chesapeake Miocene conacean gastropods. The prominent nodulose carina around the shoulders of *Calverturris* species, along with the large, evenly-spaced cords

on the body whorls, sets this genus aside from all other Transmarian mangeliine taxa. In general body form and sculpture pattern, *Calverturris* is closest to *Sediliopsis* Petuch, 1988, but differs in having larger and more inflated shells and in having the characteristic nodulose shoulder carina.

As *Calverturris* is only known from the Calvert and Choptank Formations, the genus appears to have become extinct during mid-Serravallian time.

Calverturris schmidtii new species
(figure 25)

Material examined: HOLOTYPE—Length (fragmentary) 23 mm, in Zone 17, Drum Cliff Member of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, along Patuxent River, UF 21500.

Description: Shell shape and form as outlined in genus description; shoulder earina with evenly-spaced, large nodules; single large cord present on sloping subsutural area, just posterior to nodulose carina; body whorl ornamented with 67 large spiral cords (extrapolated from fragmentary holotype); fine threads present between large spiral cords.

Etymology: Named for Mr. Robert Schmidt of Calvert County, Maryland, who collected the holotype at Jones Wharf.

Discussion: The Choptank *Calverturris schmidtii* is similar to the Calvert *C. bellaerenata*, the type of the genus, but differs in having larger and less numerous shoulder knobs and in having fine spiral threads between the large cords on the body whorl. The steeply-sloping subsutural area of *C. bellaerenata* is also smooth and devoid of spiral sculpture, while that of *C. schmidtii* is sculptured with a single large cord and several faint spiral threads.

While *Calverturris bellaerenata* is a common species in Zone 10 at Plum Point, *C. schmidtii* is a much rarer shell, with only a few fragmentary specimens having ever been collected along the Patuxent River. Apparently, the genus was already dying out by Choptank time.

Genus *Transmariaturris* new genus

Diagnosis: Shells elongately terebriform, with rounded shoulders and greatly protracted, elevated spires; siphonal canals proportionally short, stubby; subsutural area of all species slightly depressed, producing faintly indented sutural band; last whorls with smooth, unornamented shoulders; spire whorls of some species ornamented with rows of low, riblike knobs along suture margin; spire whorls of some species smooth, unornamented; body and spire whorls sculptured with only very faint, delicate spiral thread, giving shells silky texture; siphonal canals ornamented with 10–12 thin spiral cords; apertures proportionally small, oval; protoconchs unknown; anal notch shallow, with indentation corresponding to depressed subsutural band.

Type species: *Pleurotoma (Hemipleurotoma) calvertensis* Martin, 1904, Calvert Formation, Langhian Miocene of Maryland (figure 28).

Other species in *Transmariaturris*: "*Pleurotoma (Hemipleurotoma) choptankensis* Martin, 1904, Choptank Formation, Serravallian Miocene of Maryland

Etymology: A combination of "*Transmaria*", for the Transmarian Province, and "*turris*".

Discussion: Based on general shell shape, I had originally placed this compact group of elongated, terebriform turrids in the elavine genus *Chesaclava* Petuch, 1988 (Petuch, 1988:35). Further study, however has shown that these two groups of turrids differ in a number of ways and actually belong in separate subfamilies. *Transmariaturris*, although convergent on the protracted spire form of *Chesaclava*, differs from that genus in having larger, more inflated shells with proportionally larger body whorls, by having longer and better developed siphonal canals, in having more indented anal notches that produce solenozones, and in having spiral sculpturing. The small, smooth *Chesaclava* species closely resemble miniature *Cymatosyrinx* Dall, 1889 species and develop a varix-like adult lip and stromboid notch. These two characters are not seen in *Transmariaturris*.

Although the diagnostic protoconchs were missing on all *Transmariaturris* specimens examined, I have placed this new genus in the subfamily Mangeliinae, primarily on its similarity to the genus *Calverturris*. Both genera are of the same general shape and size, and share the same type of anal notch and outer lip structure. *Transmariaturris* differs from *Calverturris*, however, in lacking the large, prominent spiral cords on the body whorl and also in lacking the distinctive nodulose shoulder earina. The subsutural area of *Calverturris* is planar, while that of *Transmariaturris* is slightly depressed.

ACKNOWLEDGEMENTS

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Appendix 1. Muricacean, Buccinacean, and Conacean Higher Taxa from the Calvertian Subprovince of the Transmarian Province. T = Transmarian endemic genus, C = Caloosagenic genus, B = Boreogenic genus.

	T	C	B
Superfamily Muricea			
Family Muricidae			
Subfamily Muricinae da Costa, 1776			
<i>Phyllonotus</i> Swainson, 1833		*	
Subfamily Muricopsinae Radwin and D'Attilio, 1971			
<i>Murxiella</i> Clench and Farfante, 1945		*	
Subfamily Ocenebrinae Gray, 1847			
<i>Mariasalpinx</i> Petuch, 1988	*		
<i>Sephasalpinx</i> Petuch, 1988	*		
<i>Urosalpinx</i> Stimpson, 1865		*	
Subfamily Trophoninae Cossmann, 1903			
<i>Boreotrophon</i> Fischer, 1884			*
<i>Chesatrophon</i> Petuch, 1988	*		
<i>Lirosoma</i> Conrad, 1862	*		
<i>Patuxentrophon</i> Petuch, 1992	*		
<i>Scalaspira</i> Conrad, 1862	*		
Subfamily Typhinae Cossmann, 1903			
<i>Lacertyphis</i> Cossmann, 1903		*	
Family Thaididae			
Subfamily Ecphorinae Petuch, 1988			
<i>Chesathais</i> Petuch, 1988		*	
<i>Ecphora</i> Conrad, 1843		*	
<i>Ecphorosycon</i> Petuch, 1988	*		
<i>Triscephora</i> Petuch, 1988	*		
Superfamily Buccinacea			
Family Fasciolaridae			

Appendix 1. Continued

	T	C	B
Subfamily Fasciolarinae Gray, 1853			
<i>Buccinofusus</i> Conrad, 1868	*		
<i>Mariafus</i> Petuch, 1988	*		
Subfamily Fusininae Swainson, 1840			
<i>Pseudaptyxis</i> Petuch, 1988	*		
Family Melongenidae			
Subfamily Busyconinae Finlay and Marwick 1937			
<i>Busycotypus</i> Wenz, 1913		*	
<i>Sycopsis</i> Conrad, 1867	*		
<i>Turrifulgur</i> Petuch, 1988		*	
Family Buccinidae			
<i>Celatoconus</i> Conrad, 1862		*	
<i>Ptychosalpinx</i> Gill, 1867		*	
<i>Solenosteira</i> Dall, 1890		*	
Family Nassariidae			
<i>Bulliopsis</i> Conrad, 1862	*		
<i>Ilyanassa</i> Stimpson, 1865		*	
Family Columbellidae			
<i>Mitrella</i> Risso, 1826		*	
Superfamily Conacea			
Family Conidae			
<i>Leptoconus</i> Swainson, 1840		*	
Family Terebridae			
<i>Lacynthastula</i> Petuch, 1988	*		
<i>Strioterebrum</i> Sacco, 1891		*	
Family Turridae			
Subfamily Clavinae Powell, 1942			
<i>Chesaclava</i> Petuch, 1988	*		
<i>Cymatosyrinx</i> Dall, 1889		*	
<i>Sediliopsis</i> Petuch, 1988	*		
Subfamily Mangeliinae Fischer, 1887			
<i>Calverturris</i> Petuch, 1992 T	*		
<i>Glyphostoma</i> Gabb, 1872		*	
<i>Ocnopota</i> Möreli, 1852			*
<i>Mariadrilha</i> Petuch, 1988	*		
<i>Transmariaturris</i> Petuch, 1992	*		
Subfamily Turriculinae Powell, 1942			
<i>Chesasyrinx</i> Petuch, 1988	*		
<i>Mariaturricula</i> Petuch, 1988	*		
<i>Nodisurculina</i> Petuch, 1988	*		
Subfamily Turritinae Swainson, 1840			
<i>Hemipleurotoma</i> Cossmann, 1903	*		

Appendix 2. Muricacean, Buccinacean, and Conacean Species from the Calvertian Subprovince of the Transmarian Province. C = Calvert Formation, Ch = Choptank Formation, L = Little Cove Point Unit, S = St. Mary's Formation

	C	CH	L	S
Muricidae				
Muricinae				
¹ <i>Phyllonotus millvillensis</i> (Richards and Harbison, 1942)	*			
Muricepsinae				
<i>Murexiella shilohensis</i> (Heilprin, 1887)	*			
Ocenebrinae				
<i>Mariasalpinx emilyae</i> Petuch, 1988				*
<i>Mariasalpinx</i> new species			*	
<i>Stephanosalpinx candelabra</i> Petuch, 1988		*		
<i>Urosalpinx rusticus</i> (Conrad, 1830)			*	*
Trophoninae				
<i>Boreotrophon harasewychi</i> Petuch, 1988				*
<i>Boreotrophon laevis</i> (Martin, 1904)			*	*
<i>Boreotrophon lindae</i> Petuch, 1988				*
<i>Chesatrophon chesapeakeanus</i> (Martin, 1904)			*	*
<i>Chesatrophon</i> new species a	*			
<i>Chesatrophon</i> new species b		*		
<i>Lirosoma mariana</i> Petuch, 1988				*
<i>Patuxentrophon patuxentensis</i> (Martin, 1904)		*		
<i>Patuxentrophon</i> new species	*			
<i>Scalaspira harasewychi</i> Petuch, 1988				*
<i>Scalaspira vokesae</i> Petuch, 1988			*	
Typinae				
<i>Laevitaphis acuticosta</i> (Conrad, 1830)			*	*
<i>Laevitaphis</i> new species a	*			
<i>Laevitaphis</i> new species b		*		
Thaididae				
Ecphorinae				
<i>Chesathais ecclesiasticus</i> (Dall, 1915)	*			
<i>Chesathais lindae lindae</i> Petuch, 1988		*		
<i>Chesathais lindae donaldasheri</i> Petuch, 1989		*		
<i>Chesathais lindae drumchiffensis</i> Petuch, 1989		*		
<i>Chesathais whitfieldi</i> Petuch, 1989	*			
<i>Ecphora asheri</i> Petuch, 1988			*	
<i>Ecphora calvertensis</i> Petuch, 1988	*			
<i>Ecphora calvertensis</i> subspecies	*			
<i>Ecphora chesapeakeensis</i> Petuch, 1992	*			
<i>Ecphora choptankensis choptankensis</i> Petuch, 1988		*		
<i>Ecphora choptankensis delicata</i> Petuch, 1989		*		
<i>Ecphora choptankensis vokesi</i> Petuch, 1989		*		
<i>Ecphora gardnerae gardnerae</i> Wilson, 1987				*
<i>Ecphora gardnerae angusticostata</i> Petuch, 1989				*
<i>Ecphora germonae</i> Ward and Gilinsky, 1988			*	
<i>Ecphora meganae meganae</i> Ward and Gilinsky, 1988		*		
<i>Ecphora meganae sandgatesensis</i> Petuch, 1989		*		
<i>Ecphora rikeri rikeri</i> Petuch, 1988		*		
<i>Ecphora rikeri harasewychi</i> Petuch, 1988		*		
<i>Ecphora turneri</i> Petuch, 1992	*			
<i>Ecphora wardi</i> Petuch, 1989	*			
<i>Ecphora wardi</i> subspecies	*			
<i>Ecphora williamsi</i> Ward and Gilinsky, 1988		*		
<i>Ecphora</i> (Triscephora) <i>eccentrica</i> Petuch, 1988	*			
<i>Ecphora</i> (Triscephora) <i>martini</i> Petuch, 1988	*			
<i>Ecphora</i> (Triscephora) <i>patuxentia patuxentia</i> Petuch, 1988		*		
<i>Ecphora</i> (Triscephora) <i>patuxentia shattucki</i> Petuch, 1989		*		
<i>Ecphora</i> (Triscephora) <i>prunicola</i> Petuch, 1988	*			
<i>Ecphora</i> (Triscephora) <i>scientistensis</i> Petuch, 1992	*			
<i>Ecphora</i> (Triscephora) <i>schmidtii</i> Petuch, 1989	*			
<i>Ecphora</i> (Triscephora) <i>smithae</i> Petuch, 1988		*		
<i>Ecphora</i> (Triscephora) <i>smithae</i> subspecies	*			

Appendix 2. Continued.

	C	CH	L	S
<i>Ephora</i> (<i>Triscephora</i>) <i>tricostata</i> Martin, 1904	*			
<i>Ephorosycon kalyx</i> (Petuch, 1988)	*			
<i>Ephorosycon lindajoyceae</i> Petuch, 1992		*		
<i>Ephorosycon pamlico</i> (Wilson, 1987)	*			
<i>Ephorosycon</i> new species	*			
Fasciolaridae				
<i>Buccinofusus</i> (?) <i>calvertanus</i> (Martin, 1904)	*			
<i>Buccinofusus chesapeakeensis</i> Petuch, 1988			*	
<i>Buccinofusus deltexus</i> (Conrad, 1843)	*			
<i>Buccinofusus migrans</i> (Conrad, 1843)	*			
<i>Buccinofusus parilis</i> (Conrad, 1832)				*
<i>Buccinofusus patuxentensis</i> Petuch, 1992		*		
<i>Mariafusus marylandicus</i> (Martin, 1904)				*
<i>Pseudaptyxis sanctaemariae</i> Petuch, 1988				*
Melongenidae				
Busyconinae				
<i>Busycotypus alveatum</i> (Conrad, 1863)				*
<i>Busycotypus asheri</i> Petuch, 1988				*
<i>Busycotypus calvertensis</i> Petuch, 1988	*			
<i>Busycotypus chesapeakeensis</i> Petuch, 1988			*	
<i>Busycotypus choptankensis</i> Petuch, 1992		*		
<i>Busycotypus coronatum</i> (Conrad, 1840)				*
<i>Busycotypus rugosum</i> (Conrad, 1843)				*
<i>Sycopsis lindae</i> Petuch, 1988		*		
<i>Sycopsis tuberculatum</i> (Conrad, 1840)				*
<i>Sycopsis</i> new species a	*			
<i>Sycopsis</i> new species b			*	
<i>Turritulur fusiforme</i> (Conrad, 1840)				*
<i>Turritulur marylandicus</i> Petuch, 1992	*			
<i>Turritulur prunicola</i> Petuch, 1992	*			
<i>Turritulur turriculus</i> Petuch, 1988				*
<i>Turritulur</i> new species a		*		
<i>Turritulur</i> new species b			*	
Buccinidae				
<i>Celatoconus asheri</i> Petuch, 1988			*	*
<i>Celatoconus protractus</i> (Conrad, 1843)	*			
<i>Ptychosalpinx lienosa</i> (Conrad, 1843)	*			
<i>Ptychosalpinx lindae</i> Petuch, 1988				*
<i>Ptychosalpinx pustulosus</i> Petuch, 1988				*
<i>Ptychosalpinx</i> new species		*		
<i>Ptychosalpinx</i> new species		*		
<i>Solenosteira cumberlandiana</i> (Gabb, 1860)			*	*
<i>Solenosteira</i> new species	*	*	*	
Nassariidae				
<i>Bulliopsis integra</i> (Conrad, 1842)			*	*
<i>Bulliopsis marylandica</i> (Conrad, 1862)			*	
<i>Bulliopsis ovata</i> (Conrad, 1862)				*
<i>Bulliopsis quadrata</i> (Conrad, 1830)				*
<i>Bulliopsis subcylindrica</i> (Conrad, 1862)				*
<i>Ilyanassa calvertensis</i> (Martin, 1904)	*			
<i>Ilyanassa clongata</i> (Whitfield, 1894)		*		
<i>Ilyanassa greensboroensis</i> (Martin, 1904)		*		
<i>Ilyanassa gubernatoria</i> (Martin, 1904)	*			
<i>Ilyanassa marylandica</i> (Martin, 1904)			*	*
<i>Ilyanassa peralta</i> (Conrad, 1868)			*	*
<i>Ilyanassa peraltoides</i> (Martin, 1904)		*		
<i>Ilyanassa trivittatoides</i> (Whitfield, 1894)		*		
<i>Ilyanassa</i> new species				*
Columbellidae				
<i>Mitrella calvertensis</i> (Martin, 1904)	*			
<i>Mitrella communis</i> (Conrad, 1862)				*

Appendix 2. Continued

	C	CH	L	S
<i>Mitrella</i> new species a	*			
<i>Mitrella</i> new species b		*		
<i>Mitrella</i> new species c			*	
Conidae				
<i>Conus</i> (<i>Leptoconus</i>) <i>asheri</i> Petuch, 1988				*
<i>Conus</i> (<i>Leptoconus</i>) <i>diluvianus</i> Green, 1830				*
<i>Conus</i> (<i>Leptoconus</i>) <i>sanctamariae</i> Petuch, 1988				*
Terebridae				
<i>Laevihastula inornata</i> (Whitfield, 1894)			*	*
<i>Laevihastula marylandica</i> Petuch, 1988				*
<i>Laevihastula patuxentia</i> (Martin, 1904)		*		
<i>Laevihastula simplex</i> (Conrad, 1830)			*	*
<i>Laevihastula subvirata</i> (Conrad, 1863)			*	*
<i>Strioterebrum calvertensis</i> (Martin, 1904)	*			
<i>Strioterebrum curvilineata</i> (Whitfield, 1894)	*			
<i>Strioterebrum curvilinearata</i> (Conrad, 1843)				*
<i>Strioterebrum dalli</i> (Martin, 1904)		*		
<i>Strioterebrum sincera</i> (Dall, 1895)			*	*
<i>Strioterebrum whitfieldi</i> (Martin, 1904)	*			
Turridae				
Clavinae				
<i>Chesaclava dissimilis</i> (Conrad, 1830)				*
<i>Chesaclava pseudoburnea</i> (Whitfield, 1894)	*			
<i>Chesaclava quarlesi</i> Petuch, 1988				*
<i>Chesaclava whitfieldi</i> (Martin, 1904)	*			
<i>Chesaclava</i> new species	*	*		
<i>Cymatosyrinx limatula</i> (Conrad, 1830)			*	*
<i>Cymatosyrinx mariana</i> Petuch, 1988				*
<i>Cymatosyrinx pyramidalis</i> (Martin, 1904)				*
<i>Cymatosyrinx</i> new species a	*			
<i>Cymatosyrinx</i> new species b		*		
<i>Sediliopsis angulata</i> (Martin, 1904)				*
<i>Sediliopsis calvertensis</i> (Martin, 1904)	*			
<i>Sediliopsis distans</i> (Conrad, 1862)				*
<i>Sediliopsis gracilis</i> (Conrad, 1830)				*
<i>Sediliopsis inciliifera</i> (Conrad, 1830)			*	
<i>Sediliopsis patuxentia</i> (Martin, 1904)		*		
Mangelinae				
<i>Calverturris bellacrenata</i> (Conrad, 1841)	*			
<i>Calverturris schmidtii</i> Petuch, 1992		*		
<i>Glyphostoma obtusa</i> (Martin, 1904)	*			
<i>Oenopota cornuchana</i> (Martin, 1904)	*			
<i>Oenopota marylandica</i> (Petuch, 1988)				*
<i>Oenopota parva</i> (Conrad, 1830)			*	*
<i>Mariadrillia parvolda</i> (Martin, 1904)				*
<i>Transmariaturris calvertensis</i> (Martin, 1904)	*			
<i>Transmariaturris choptankensis</i> (Martin, 1904)		*		
Turriculinae				
<i>Chesasyrinx mariana</i> (Martin, 1904)				*
<i>Chesasyrinx rotifera</i> (Conrad, 1830)				*
<i>Chesasyrinx</i> new species	*	*		
<i>Mariaturricula marylandica</i> (Conrad, 1834)				*
<i>Mariaturricula biscatenaria</i> (Conrad, 1811)	*			
<i>Mariaturricula rugata</i> (Conrad, 1862)		*		
<i>Mariaturricula</i> new species a	*			
<i>Mariaturricula</i> new species b	*			
<i>Mariaturricula</i> new species c		*		
<i>Mariaturricula</i> new species d			*	
<i>Nodisurculina engonata</i> (Conrad, 1862)				*
Turritinae				
<i>Hemipleurotoma communis</i> (Conrad, 1830)			*	*

Appendix 2. Continued

	C	CH	L	S
<i>Hemipleurotoma protocommunis</i> (Martin, 1904)	*			
<i>Hemipleurotoma</i> new species		*		

¹ Known from the Calvert-equivalent Kirkwood Formation of New Jersey, possibly occurring in the Calvert Formation

Publication Dates of *The Nautilus*

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As the publication dates of earlier issues of *The Nautilus* are nowhere readily accessible, the purpose of this note is to provide this information in a single comprehensive listing.

Although six indices have been published for *The Nautilus* and for its predecessor, *The Conchologists' Exchange* (Pilsbry & Johnson, 1895; Henderson, 1927; La Rocque, 1951, 1963, 1972; Abbott, 1979), none provide a listing of publication dates. The dates listed below are compiled from a variety of sources.

Dates for issues published during Henry A. Pilsbry's tenure as Editor (volume 3, number 1, to volume 71, number 3) were determined largely from his published bibliographies (American Malacological Union, 1940; Baker, 1958; Clench & Turner, 1962), and are identified by an asterisk (*) following the date. As noted in the first of these bibliographies (American Malacological Union, 1940:4), the dates for volumes 13-45 inclusive were derived from ledgers maintained by Charles W. Johnson, then Managing Editor.

Publication dates of issues prior to volume 13, as well as of volume 46, number 1, had been extrapolated based on the dates of receipt of these issues by several libraries (American Malacological Union, 1940:4). These dates, identified by a dagger (†), are estimates and may in some cases prove to be one or more days later than the actual date of publication.

During H. Burrington Baker's association with *The Nautilus*, first as Business Manager (volume 46, number 2, to volume 71, number 3) then as Editor and Editor Emeritus (volume 71, number 4, to volume 84, number 1), publication dates for a volume were published in the "Notes and News" section of the first or second issue of the subsequent volume. This practice was continued by the succeeding editor R. Tucker Abbott (volume 83, number 1, to volume 100, number 4) for volume 85. Dates determined from these listings are marked by a double dagger (‡) following the date.

Exact dates for volumes 86-89 have not previously been published. Mailing dates for these issues were determined from records on file in the editorial offices of the journal (PS Forms 3541 and 3542), are identified by a section mark (§).

Beginning with volume 90, dates of publication were printed on the cover and/or title page of every issue, and are not included here.

Dates derived from the bibliography of W. H. Dall (Bartsch *et al.*, 1946), identified by a number sign (#),

supplement and/or corroborate the dating of the earliest issues. For issues that could not be dated in any other manner, the date of the library stamp of the Library of Congress (identified as LC), the National Museum of Natural History (identified as USNM) the Museum of Comparative Zoology, Harvard University (identified as MCZ), or the Boston Society of Natural History (identified as BSNH, now in the library of R. Tucker Abbott) is provided.

The Conchologists' Exchange

- 1(1): July 1886
- 1(2): August 1886
- 1(3): 27 September 1886 LC
- 1(4): October 1886
- 1(5): 6 December 1886 †
- 1(6): after 28 December 1886 †
- 1(7): January 1887 [February 25 LC]
- 1(8): February 1887 [March 9 LC]
- 1(9/10): 30 April 1887 USNM
- 1(11): May 1887
- 1(12): 28 June 1887 LC

- 2(1): 20 July 1887 MCZ [10 August #, 12 August LC]
- 2(2): August 1887 [15 September LC]
- 2(3): September 1887 [13 October LC]
- 2(4): October 1887 [5 November LC, USNM]
- 2(5): November 1887 [15 December LC]
- 2(6): December 1887 [23 January 1888 LC]
- 2(7): January 1888 [20 February LC]
- 2(8): February 1888 [26 March LC]
- 2(9): 2 May, 1888 † [7 May LC]
- [Publication suspended.]

The Nautilus

- 3(1): 5 May 1889 †, #
- 3(2): 9 June 1889 †
- 3(3): 14 July 1889 †, #
- 3(4): 11 August 1889 †
- 3(5): 1 October 1889 †
- 3(6): 18 October 1889 †
- 3(7): 13 November 1889 †
- 3(8): 7 January 1890 †
- 3(9): 11 February 1890 †, #
- 3(10): 12 March 1890 †
- 3(11): 15 April 1890 †
- 3(12): 7 May 1890 †

- 4(1): 9 June 1890 †
- 4(2): 27 June 1890 †

4(3): 6 July 1890 †
 4(4): 5 August 1890 †
 4(5): 1 October 1890 †
 4(6): 14 October 1890 †
 4(7): 7 November 1890 †
 4(8): 22 December 1890 †, #
 4(9): 11 January 1891 †
 4(10): 1 February 1891 †
 4(11): 4 March 1891 †
 4(12): 5 April 1891 †

5(1): 19 May 1891 †, #
 5(2): 17 June 1891 †, #
 5(3): 10 July 1891 †, #
 5(4): 19 August 1891 †, #
 5(5): 17 September 1891 †
 5(6): 18 October 1891 †
 5(7): 18 November 1891 †
 5(8): 9 December 1891 †
 5(9): 14 January 1892 †, #
 5(10): 5 February 1892 †
 5(11): 25 March 1892 †, #
 5(12): 17 April 1892 †

6(1): 15 May 1892 †
 6(2): 1 June 1892 †
 6(3): 6 July 1892 †
 6(4): [?] August 1892 †
 6(5): 11 September 1892 †
 6(6): 4 October 1892 †
 6(7): 8 November 1892 †
 6(8): 12 December 1892 †
 6(9): 12 January 1893 †
 6(10): 10 February 1893 # [12 February †]
 6(11): [?] March 1893 †
 6(12): 9^o April 1893 † [10 April MCZ]

7(1): 7 June 1893 †
 7(2): 19 June 1893 †
 7(3): 17 July 1893 †
 7(4): 15 August 1893 †
 7(5): 3 September 1893 †, #
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 17(3): 3 July 1903 •
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 20(12): 12 April 1907 •, #

 21(1): 13 May 1907 •
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 21(4): 16 August 1907 •
 21(5): 18 September 1907 •
 21(6): 10 October 1907 •
 21(7): 7 November 1907 •
 21(8): 9 December 1907 •, # [issue mislabeled as vol. 22]
 21(9): 3 January 1908 •, # [issue mislabeled as vol. 22]
 21(10): 3 February 1908 • [issue mislabeled as vol. 22]
 21(11): 7 March 1908 •, #
 21(12): 4 April 1908 •, #

 22(1): 9 May 1908 •, #
 22(2): 12 June 1908 •
 22(3): 16 July 1908 •, #
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 22(11): 11 March 1909 •, #
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 23(11): 15 April 1910 •, #
 23(12): - never issued

 24(1): 19 May 1910 •, #
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 24(3): 6 July 1910 •, #
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 24(7): 14 November 1910 •

24(8): 12 December 1910 •, #
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 24(10): 4 February 1911 •, #
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25(1): 19 May 1911 •
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 25(12): 13 April 1912 •

26(1): 11 May 1912 •
 26(2): 1 June 1912 •
 26(3): 12 July 1912 •
 26(4): 5 August 1912 •
 26(5): 6 September 1912 •, # [issue mislabeled as no. 4]
 26(6): 10 October 1912 •
 26(7): 11 November 1912 •
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 26(9): 4 January 1913 •, #
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 26(11): 4 March 1913 •, #
 26(12): 2 April 1913 •, #

27(1): 8 May 1913 •
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 27(10): 9 February 1914 •
 27(11): 19 March 1914 •, #
 27(12): 16 April 1914 •

28(1): 16 May 1914 •, #
 28(2): 13 June 1914 •, #
 28(3): 10 July 1914 •
 28(4): 17 August 1914 •
 28(5): 22 September 1914 •, #
 28(6): 15 October 1914 •, # [issue mislabeled as no. 5]
 28(7): 20 November 1914 •
 28(8): 21 December 1914 •
 28(9): 20 January 1915 •
 28(10): 18 February 1915 •
 28(11): 10 March 1915 •, #
 28(12): 16 April 1915 •, #

29(1): 19 May 1915 •
 29(2): 3 June 1915 •
 29(3): 6 July 1915 •
 29(4): 4 August 1915 •
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 29(6): 11 October 1915 •
 29(7): 10 November 1915 •
 29(8): 17 December 1915 •

29(9): 7 January 1916 •
 29(10): 1 February 1916 •, #
 29(11): 6 March 1916 •
 29(12): 8 April 1916 •

30(1): 19 May 1916 •, #
 30(2): 5 June 1916 •
 30(3): 14 July 1916 •, #
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 30(6): 6 November 1916 •
 30(7): 4 December 1916 •
 30(8): 30 December 1917 •
 30(9): 20 January 1917 •
 30(10): 6 March 1917 •
 30(11): 29 March 1917 •
 30(12): 7 May 1917 •

[THE NAUTILUS changes to a quarterly publication schedule.]

31(1): 14 July 1917 •, #
 31(2): 18 October 1917 •
 31(3): 14 January 1918 •
 31(4): 5 May 1918 •

32(1): 20 July 1918 •, #
 32(2): 22 October 1918 •
 32(3): 17 January 1919 •, #
 32(4): 5 May 1919 •

33(1): 16 July 1919 •, #
 33(2): 6 November 1919 •
 33(3): 22 January 1920 •, #
 33(4): 20 April 1920 •

34(1): 19 July 1920 •, #
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 34(4): 5 May 1921 •, #

35(1): 26 July 1921 •, #
 35(2): 5 December 1921 •, #
 35(3): 23 January 1922 •, #
 35(4): 24 April 1922 •

36(1): 24 July 1922 •, # [issue mislabeled as vol. 35]
 36(2): 7 October 1922 •, #
 36(3): 22 January 1923 •
 36(4): 14 April 1923 •

37(1): 23 July 1923 •, #
 37(2): 11 October 1923 •, #
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39(1): 8 July 1925 •, #
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- 40(1): 12 July 1926 •
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- 41(1): 23 July 1927 •
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- 43(1): 11 July 1929 •
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 43(4): 24 April 1930 •
- 44(1): 17 July 1930 •
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- 45(1): 13 July 1931 •
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 45(3): 9 January 1932 •
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- 46(1): 20 July 1932 BSN11 [23 July †]
 46(2): 22 October 1932 ‡
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- 47(1): 16 June 1933 ‡
 47(2): 1 November 1933 ‡
 47(3): 26 January 1934 ‡
 47(4): 4 May 1934 ‡
- 48(1): 10 July 1934 ‡
 48(2): 15 October 1934 ‡
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- 49(1): 22 July 1935 ‡
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- 54(1): 23 July 1940 ‡
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- 63(1): 19 September 1949 ‡
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- 64(1): 5 July 1950 ‡
 64(2): 27 October 1950 ‡
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- 65(1): 27 August 1951 ‡
 65(2): 9 November 1951 ‡
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- 66(1): 25 July 1952 ‡
 66(2): 17 November 1952 ‡
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67(1): 24 July 1953 ‡
 67(2): 11 November 1953 ‡
 67(3): 18 February 1954 ‡
 67(4): 17 May 1954 ‡
 68(1): 24 July 1954 ‡
 68(2): 15 November 1954 ‡
 68(3): 11 February 1955 ‡
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 70(1): 13 August 1956 ‡
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 71(2): 4 November 1957 •, ‡
 71(3): 4 March 1958 ‡
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 72(2): 1 October 1958 ‡
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80(3): 24 January 1967 ‡
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 83(2): 31 October 1969 ‡
 83(3): 23 January 1970 ‡
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 84(1): 16 July 1970 ‡
 84(2): 5 October 1970 ‡
 84(3): 25 January 1971 ‡
 84(4): 26 April 1971 ‡
 85(1): 20 July 1971 ‡
 85(2): 4 October 1971 ‡
 85(3): 27 January 1972 ‡
 85(4): 28 April 1972 ‡
 86(1): 27 July 1972 §
 86(2-4): 1 December 1972 §

[Publication changes to one volume per calendar year.]

87(1): 24 January 1973 §
 87(2): 27 April 1973 §
 87(3): 30 July 1973 §
 87(4): 4 October 1973 §
 88(1): 29 January 1974 §
 88(2): 30 April 1974 §
 88(3): 22 July 1974 §
 88(4): 25 October 1974 §
 89(1): 31 January 1975 §
 89(2): 30 April 1975 §
 89(3): 18 July 1975 §
 89(4): 29 October 1975 §

[Subsequent issues have dates of publication printed on the title page and generally also on the cover.]

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of $8\frac{1}{2} \times 11$ inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda, MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgements, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, . . . , NOT figs. 1a, 1b, 1c, . . . NOR plate 1, fig. 1 . . .). Illustrations must be arranged in proportions that will conform with the width of a page ($6\frac{3}{4}$ inches or 171 mm) or a column ($3\frac{3}{4}$ inches or 92 mm). The maximum size of a printed figure is $6\frac{3}{4}$ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

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An order form for reprints will accompany the proofs. Reprints may be ordered through the editor.

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